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## Marine Vertebrate Remains from Middle-late Devonian Bone Beds at Little Hardwick Creek in Vaughns Mill, Kentucky and at The East Liberty Quarry in Logan County, Ohio

John M. James  
*Wright State University*

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MARINE VERTEBRATE REMAINS FROM MIDDLE-LATE DEVONIAN BONE  
BEDS AT LITTLE HARDWICK CREEK IN VAUGHNS MILL, KENTUCKY AND  
AT THE EAST LIBERTY QUARRY IN LOGAN COUNTY, OHIO

A thesis submitted in partial fulfillment of the requirements for the degree of Master of  
Science

By

John M. James  
B.A., Wright State University, 2006

2011  
Wright State University

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JOHN M. JAMES

2011

WRIGHT STATE UNIVERSITY

GRADUATE SCHOOL

August 22, 2011

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY  
SUPERVISION BY John M. James ENTITLED Marine Vertebrate Remains from  
Middle-Late Devonian Bone Beds at Little Hardwick Creek in Vaughns Mill, Kentucky  
and at the East Liberty Quarry in Logan County, Ohio BE ACCEPTED IN PARTIAL  
FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of  
Science.

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Andrew Hsu, Ph.D.  
Dean, Graduate School

## Abstract

James, John M. M. S., Department of Earth and Environmental Sciences, Wright State University, 2011. MARINE VERTEBRATE REMAINS FROM MIDDLE-LATE DEVONIAN BONE BEDS AT LITTLE HARDWICK CREEK IN VAUGHNS MILL, KENTUCKY AND AT THE EAST LIBERTY QUARRY IN LOGAN COUNTY, OHIO.

Stratigraphic, lithologic, faunal and conodont biozone analysis will provide insight to whether or not East Liberty Bone Bed, in Logan County, Ohio, and Little Hardwick Creek Bone Bed C, in Vaughns Mill, Kentucky, are chronostratigraphic correlations to one another; they are separated by 370 kilometers (230 miles).

Material from each bed was collected and broken down in acid and analyzed. Remaining residue after acid treatment was analyzed under a dissecting microscope for lithological and fossil contents, identified from previous fossil vertebrate findings at other locations.

Final analysis of these beds showed that lithologically and faunally they are very similar. However, conodonts observed in the beds placed East Liberty Bone Bed within the *linguiformis* conodont biozone (376-376.5 ma) and Little Hardwick Creek Bone Bed C within the *triangularis* conodont biozone (374-376 ma). Therefore, East Liberty Bone Bed and Little Hardwick Creek Bone Bed C do not chronostratigraphically correlate to one another. To determine if there is a chronostratigraphic correlation between East Liberty and Little Hardwick Creek, future studies should focus on bone beds A and B at Little Hardwick Creek to determine if there is a chronostratigraphic correlation between East Liberty Bone Bed and Bone Beds A and B at Little Hardwick Creek.

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## **Chapter 1: Introduction**

A paleontologically important, well preserved macro- and micro-vertebrate fauna was obtained from a bone bed at the boundary between the Middle Devonian, Givetian Stage, Deleware Limestone and the Late Devonian, Frasnian Stage, Ohio Shale in East Liberty, Ohio. The exposure occurs at the uppermost portions of the East Liberty Quarry, Logan Co., OH, located adjacent to U.S. Highway 33. The quarry exposes approximately 6 meters of the Deleware Limestone overlain by 5 meters of the Late Devonian Ohio Shale. In spots the Ohio Shale is overlain by the Late Devonian, Frasnian Stage, Olentangy Shale (Fig. 1).

Eon	Era	Period	Epoch	Age	Age Ma
Phanerozoic	Paleozoic	Devonian	Upper/Late	Famennian	359.2 ± 2.5
				Frasnian	374.5 ± 2.6
			Middle	Givetian	385.3 ± 2.6
				Eifelian	391.8 ± 2.7
				Emsian	397.5 ± 2.7
			Lower/Early	Pragian	407.0 ± 2.8
				Lochkovian	411.2 ± 2.8
					416.0 ± 2.8

Figure 1. Stages for the Devonian (C. Ciampaglio).

This bone rich bed occurs within a distinct, 6 cm layer that spans portions of the exposure. The lithology of the layer consists of a maroon-gray to brownish-gray, fine to medium-crystalline dolomitic limestone. Copious well preserved macro- and micro-vertebrate remains and phosphatic nodules are scattered primarily on the upper surface and within the upper two -to- three centimeters of the layer.

Macro-vertebrate remains include disarticulated arthrodire plates and isolated skeletal elements, as well as sarcopterygian tooth plates and teeth. Micro-vertebrate material consists of abundant conodont elements, acanthodian and paleonisciform actinopterygians scales, chondrichthyan dermal denticles and teeth. Chondrichthyans are represented by the cladoselelachs *Stethacanthus*, *Symmorium*, cladodonts, by the phoebodontids *Phoebodus* and by members of the genus *Protacrodus*, as well as several undescribed species.

While the East Liberty bone-bed has been assigned to the Columbus Limestone (Wells, 1944), comparison of the inclusive fauna with that of the traditional Columbus Bone Beds, show that this is clearly not the case. The vertebrate fauna of the East Liberty Bone Bed appears to be similar to the bone bed that is exposed at the Little Hardwick Creek, Vaughns Mill, Kentucky. Given this similarity, this study will focus on the comparison between the East Liberty Bone Bed and the Late Devonian, Frasnian Stage, Little Hardwick Creek Bone Bed with analysis on lithostratigraphy, sequence stratigraphy, biostratigraphy and faunal correlation.

## **Chapter 2: Historical Context of Ohio and Kentucky during the Middle and Late Devonian**

### **2.1 Introduction**

The Devonian System of rocks exposed in Ohio are found along a north-south band running through the central portion of Ohio, trending to the northeastern portion of the state and along portions of the northwestern counties.

The Early Devonian is not well represented in Ohio. The Middle Devonian system consists of limestones and dolomites suggesting a shallow sea, while the the Late Devonian system consists of black shales which suggest a paleoenvironment consisting of deep seas. Within the Middle and Late Devonian rocks, bone beds can be found which give valuable insight into life during the Devonian, as well as early appearances of the chondrichthyans, lending insight into their evolutionary beginnings.

Devonian age rocks are located across the east-central and eastern portions of Kentucky along the flanks of the Cincinnati Arch (Fig. 2).

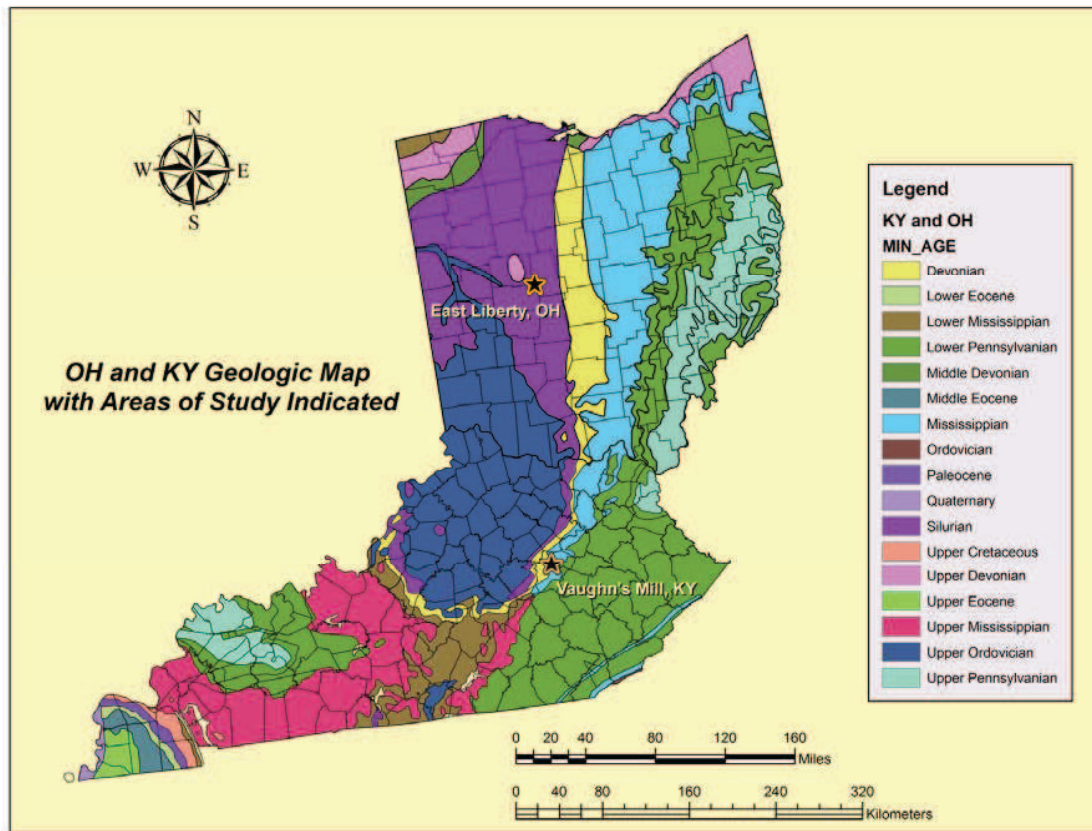


Figure 2 Geologic map of Ohio and Kentucky showing the extent of the Devonian (C. Ciampaglio).

As in Ohio, Kentucky has very few exposures of Early Devonian rocks but is well represented by Middle Devonian and Late Devonian rocks.

## **2.2 Paleogeography of Ohio and Kentucky**

Fossil content, lithology, as well as modern sedimentary ecological settings observed today, indicate Ohio and Kentucky were located near the equator during the Late-Middle Devonian. Marine invertebrates, in limestones and shales, are readily observed in the Devonian rocks of Ohio and Kentucky. Many of these taxa, especially corals, favor warm, clear, shallow tropical seas which today can be found 15°-30° above and below the equator (Prothero, 2004) (Fig. 3 (Fig. 4).



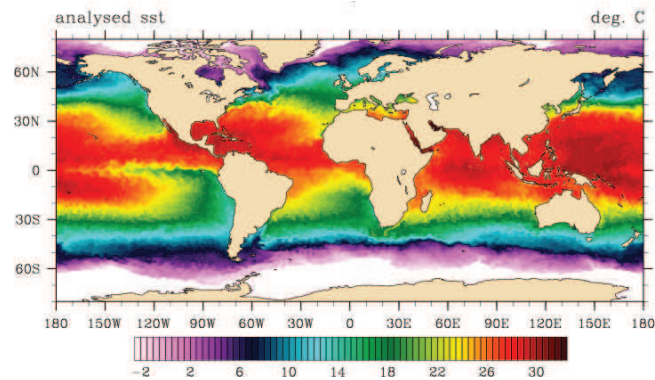


Figure 3 Present-day surface water temperatures. Corals are almost exclusively found within 15°-30° north and south latitude of the equator.

“Odyssey L4 Global Analysis,” *Marine Environment and Security for the European Area*, 30 March, 2009.

[http://www.mersea.eu.org/Satellite/sst\\_validation.html](http://www.mersea.eu.org/Satellite/sst_validation.html)

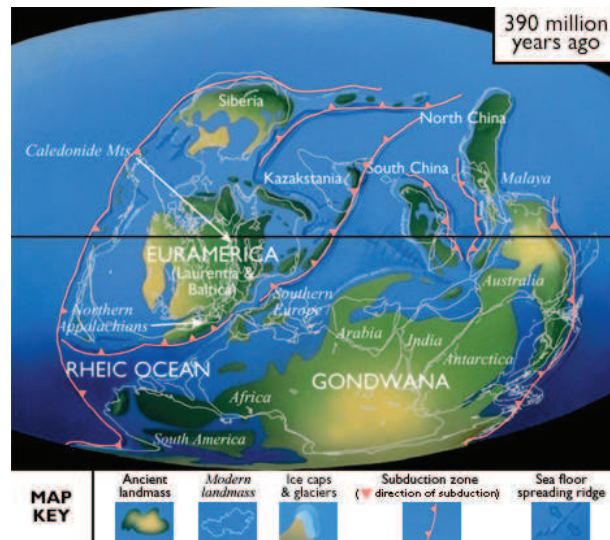


Figure 4 Devonian paleogeography. Arrow indicates approximate location of Ohio and Kentucky, which both appear to lie within 15°-30° north and south latitudes.

“The Devonian,” *The Paleontology Portal*.

[http://www.paleoportal.org/index.php?globalnav=time\\_space&sectionnav=period&period\\_id=13](http://www.paleoportal.org/index.php?globalnav=time_space&sectionnav=period&period_id=13).

### **2.3 Geology of Ohio and Kentucky**

Devonian rocks in Ohio can be found in a north-south band in the central part of the state (Fig. 2), curving to the northwest. Devonian rocks can also be observed along the Erie shore from Sandusky to Ashtabula. The Bellefontaine Outlier, in Logan County, contains Late-Middle Devonian rocks. The term outlier was applied to this region because the rocks surrounding the Bellefontaine Outlier are considerably older (mostly Silurian) with the closest Devonian rocks, other than those forming the outlier, being found at least thirty miles away in any direction (Hansen, 1999).

Devonian rocks in Kentucky can be found in scattered outcrops in east-central to eastern Kentucky (Fig. 3). Typically Late-Middle Devonian rocks observed in Kentucky are found along the eastern and western flanks of the Cincinnati Arch (Kepferle, 2001).

The Columbus Limestone in central Ohio correlates with the Jeffersonville Limestone in Kentucky. These formations range from Emsian-Eifellian in age. The Columbus Limestone is typically buff to gray in color (Camp, 2006). The maximum thickness of the unit reaches 32 meters. The Columbus Limestone contains two members: Marlbehead Member and Venice Member. The Columbus Limestone can be further subdivided into upper and lower units (Fig. 5).

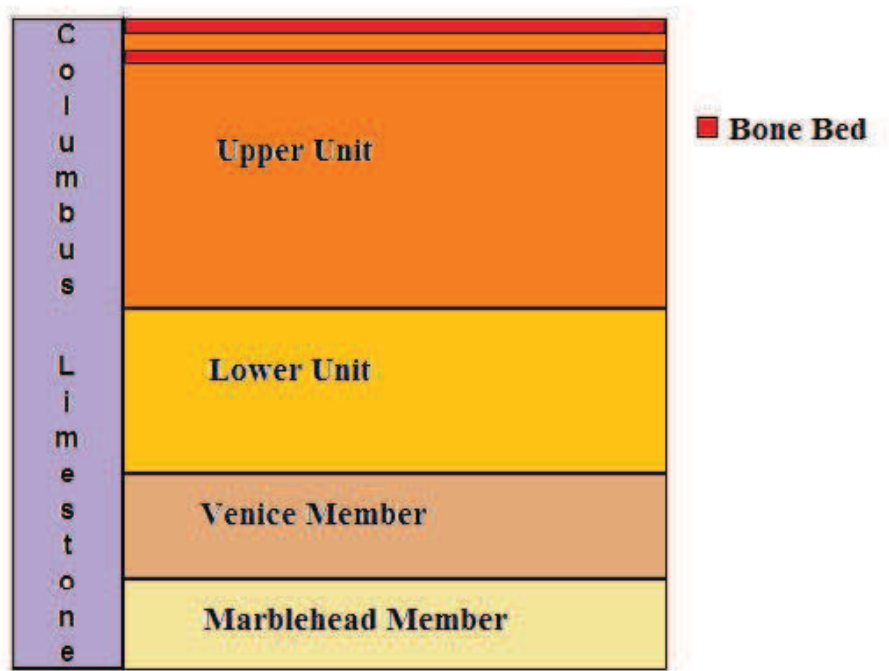


Figure 5 Divisions of the Columbus Limestone

The lower unit is 45 feet thick with massive bedding containing small pockets of calcite and small masses of chert. The upper part is 65 feet thick and is a purer limestone than the lower unit. The upper unit is even bedded with distinct chert beds and smooth layers, where slickensides are present (Stauffer, 1911). Two bone beds can be observed in the upper unit of the Columbus Limestone. The first bone bed is 6-8 inches below the boundary of the upper unit. The second bone bed marks the boundary between the Columbus and Delaware Limestones. The bone beds consist of fragments of conodonts, fish and chondrichthyan scales, teeth, spines, and bone fragments of fish (Wells, 1944; Camp, 2006).

The correlative Jeffersonville Limestone extends just below the boundary between the Early and Middle Devonian. Conkin et. al. (1988) have performed extensive work on the Jeffersonville Limestone correlating this unit to those in Ohio, New York, and Ontario, Canada (Columbus Limestone and Onondaga Limestone) using fossils (brachiopods, corals and bryozoans), bone beds, bentonite beds and paracontinuities. Conkin et. al. (1988) divided the Jeffersonville Limestone into several different zones, in ascending order; the zones are *Emmonsia ramose* Zone (The Lower Coral Zone), *Amphipora ramose* Zone (Upper Coral Zone), *Brevispirifer gregarious-Moellerina greenei* Zone, and *Paraspirifer acuminatus* Zone (Conkin et. al., 1998) (Fig. 6).

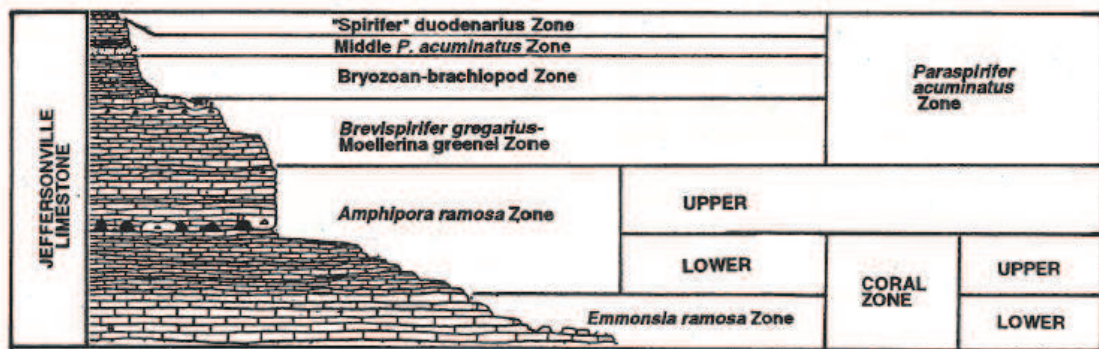


Figure 6 Different units within the Jeffersonville Limestone found at the Falls of Ohio (from Conkin et al., 1998).

The Jeffersonville Limestone is fossiliferous, dolomitic and cherty in some areas, and is typically light gray to brown in color. Conkin et al. (1988) proposed that four bone beds exist within the Jeffersonville Limestone (Conkin et. al., 1998).

The Delaware Limestone overlies the Columbus Limestone in Ohio. This argillaceous, cherty bluish-gray limestone has a maximum thickness of 11 meters. Silt sized quartz grains and terrigenous clay, a result of tectonic events in the east, is responsible for the blue color of the Delaware Limestone (Stauffer, 1911; Hanson, 2007).

Two bone beds can be observed in the Delaware Limestone. The first bone bed is approximately 40-45 centimeters below the boundary of the Delaware Limestone and the Ohio Shale. The thickness of this bone bed is 2-3 centimeters. The second bone bed is located at the boundary between the Delaware Limestone and the Ohio Shale. This bone bed is 2-3 centimeters in thickness (Wells, 1944; Camp, 2006).

The Delaware Limestone of Ohio correlates with that of the Sellersburg Limestone of Kentucky (Savage, 1931). The Sellersburg Limestone is divided into the Silver Creek and Beechwood Members (Cohee et. al., 1972). The Silver Creek Member is the lower unit in the Sellersburg Limestone, and consists of a fine grained, fossiliferous limestone, with massive beds. These beds can range up to 5 meters in thickness. Middle Devonian in age, the Silver Creek Member underlies the Beechwood Member of the Sellersburg Limestone. The Beechwood Member can be divided into two portions, a lower and upper portion. The lower portion is light gray and has a coarse crystalline texture. The upper portion is dark gray with a fine to coarse crystalline texture. The

Beechwood Member contains brachiopods, pelecypods, bryozoans and crinoids (Butts, 1915).

The Ohio Shale is Late Devonian in age. The Ohio Shale can be divided into four members: Olentangy Shale Member, Huron Shale Member, Cleveland Shale Member and the Bedford Shale Member. The Olentangy Shale Member consists of a lower gray shale unit, and an upper greenish gray shale unit (Roen et. al., 1998). The Olentangy Shale Member is a soft, argillaceous shale reaching up to 9.1 meters thick some areas. The Olentangy Shale marks the first unit in Ohio that is of Late Devonian Age. The Olentangy Shale marks a significant change in lithological character. Middle Devonian rocks are composed of limestone and dolomitic chert pockets. The Olentangy Shale is rich in terrigenous material. The Olentangy Shale also marks a vast difference in depositional environments (Stauffer, 1911; Camp 2006).

The change from Middle Devonian limestones to Late Devonian dark shales represents a change in depth of sea water. The Middle Devonian limestones were formed in a high energy, shallow water environment, which is indicated by their fossil content, corals, bryozoans, brachiopods and crinoids. Brachiopods, corals, bryozoans and crinoids are unable to persist in deep water environments due to their feeding mechanisms. Since fossils representing these taxa are absent from the Late Devonian dark shales (and in addition to their organic rich content), this allows for the interpretation that the Middle Devonian in Ohio and Kentucky was covered by a shallow sea, while in the Late Devonian of Ohio and Kentucky the sea was of deeper proportions (Hanson, 2007).

The Ohio Shale is a thick black, fissile shale that can range in thickness up to 500 feet. The formation of these shales can be attributed to an abundance of organic material



in a deprived oxygen environment. During the Late Devonian in Ohio and Kentucky the epeiric seas were restricted due to the Acadian orogeny to the east. Restriction of the seas led to stagnation and low oxygenation. The poorly oxygenated water resulted from the lack of upwelling and down-welling, creating a zone of oxygenic top-waters and a zone of anoxic bottom waters. The upper-waters eventually became anoxic as the number of phytoplankton decreased. This allowed the remaining oxygenated waters to be depleted by the remaining marine organisms inhabiting the waters. Anoxic waters caused the cessation of microbial activity and allowed organic material to accumulate, producing the characteristic Devonian black shales found in Ohio and Kentucky (Stauffer, 1911; Camp, 2006).

The New Albany Shale of Kentucky correlates to the Ohio Shale. The New Albany Shale can be divided into five members: Blocher Member, Selmier Member, Morgan Trail Member, Camp Run Member, Sanderson Member. The Blocher Member is thin laminated black shale that contains small lenses of sandstone. The Blocher Member commonly ranges in thickness from 2.5-3.0 meters (Campbell, 1946). The Blocher Member correlates to the lower unit within the Olentangy Shale in Ohio (Conkin et. al., 1998).

The Selmier Member is gray shale and contains thin beds of dolomite, limestone and quartzose sandstones (Shaver et al., 1986). The Selmier Member correlates to the upper unit belonging to the upper unit belonging to the Olentangy Shale Member in Ohio (Conkin, 1985) (Fig. 7).

		Ohio Formation	Member	Kentucky Formation	Member	Stages
D E V O N I A N	Upper	Ohio Shale	Olentangy Shale	New Albany Shale	Selmier	Famennian
					Blocher	Frasnian
	Middle	Delaware Limestone		Sellersburg Limestone	Beechwood	Givetian
					Silver Creek	
		Columbus Limestone		Jeffersonville Limestone		Eifelian

Figure 7. Correlative units of the Middle-Late Devonian in Ohio and Kentucky. Colors represent the correlative units between formations and members in Ohio and Kentucky. (Stauffer, 1911; Savage, 1931; Conkin, 1985; Conkin et al., 1998; Camp, 2006).

## Ch. 3: Paleozoic Vertebrates

### 3.1 Introduction

During the Devonian Period the overall ‘look’ of the oceans changed drastically. Gnathostomes, or jawed-fishes were the most diverse group of vertebrates that inhabited both marine and freshwater realms during the Devonian. The “fishes” have held this distinction since then. The first rise in evolutionary radiation among the chondrichthyans occurred in the Devonian. While these taxa were not like those of today, they did share many similarities. Most chondrichthyans only reached a couple of meters in size during this period of time. Some fed on fish and others fed on small invertebrates.

The apex predators of the Devonian sea were placoderms. Placoderms existed in variable environments and grew to a wide range of sizes. The most notable, *Dunkleosteus*, grew up to 10 meters in length. These marine vertebrates preyed on a varied diet including one another. As dominate as these early marine vertebrates were they only lasted a brief time in geological history falling victims to the extinction event at the end of the Devonian.

Conodonts were a staple throughout the Paleozoic Era. These animals left behind innumerable parts of their feeding apparatus. These remains are very significant in the role of biostratigraphy due to their rapidly evolving morphology, wide geographical distribution, abundance, and preservation potential (Nichols, 1999). For as small as these primitive vertebrates were, they were highly complex.

Chondrichthyes during the Paleozoic were not what we think of today. During their early evolution, Chondrichthyes experimented with different body designs and tooth

functions. The concentrations of seawater during the Permian didn't contain high enough concentrations of phosphate to allow prominent feature observed in sharks today, revolving dentition. Chondrichthyes during the Permian began developing some of the features that are found with modern sharks, such as hyostylic jaws, piercing teeth and bodies covered in dermal denticles.

### **3.2: Identifying Characteristics for Chondrichthyan Material**

Chondrichthyan material found in macroscopic material and residual material included scales and teeth. Chondrichthyan teeth found belonged to Protacrodonts, and Phoebodontids. Scales found were either undifferentiated or belonged to *Ohiolepis newberryi*, identified from comparisons to type specimen. Protacrodont teeth have a main cusp flanked by smaller lateral cusps. The cusps have bifurcating ridges (Fig. 8) (Zangerl, 1981; Turner, 1982; Ginter, 2001; Ginter, 2002;). Phoebodontid teeth are of cladodont style (Fig. 9). *Phoebodus* teeth have a central cusp that is not larger than the lateral cusps. The lateral cusps are tilted away from the central cusp at an angle between 30° and 45° (Zangerl, 1981; Turner, 1982; Ginter, 1990; Long, 1990; Lelievre et al., 1998; Ginter, 2001; Ginter, 2002). Symmoriid lateral cusps are less than 30° tilted away from the central cusp. *Symmorium* teeth are smaller than *Stethacanthus* teeth (Zangerl, 1981; Lelievre et al., 1998; Ginter, 2002).

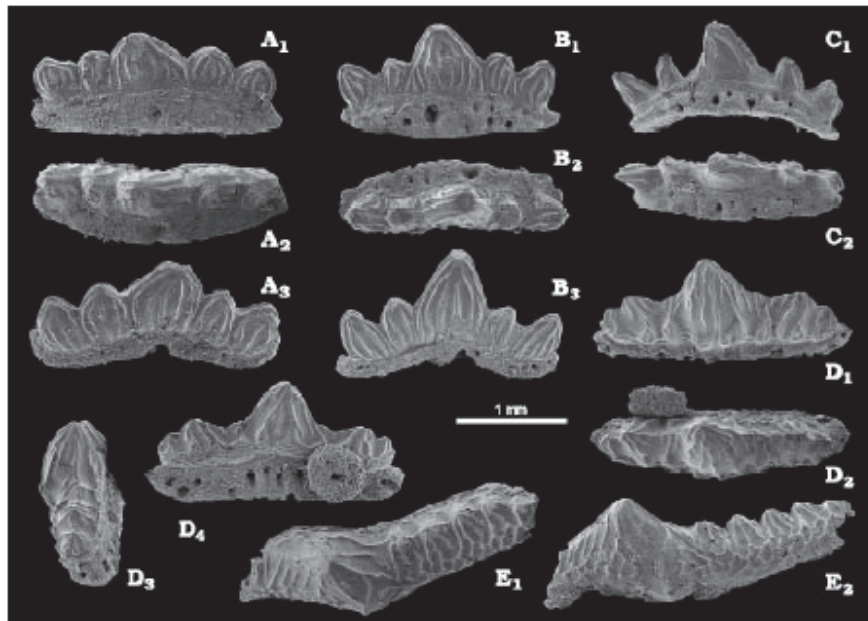


Figure 8. Examples of different *Protacrodus* sp. found in the Middle Tournaisian of Muhua, China in the Muhua Formation from Ginter et al., 2007.

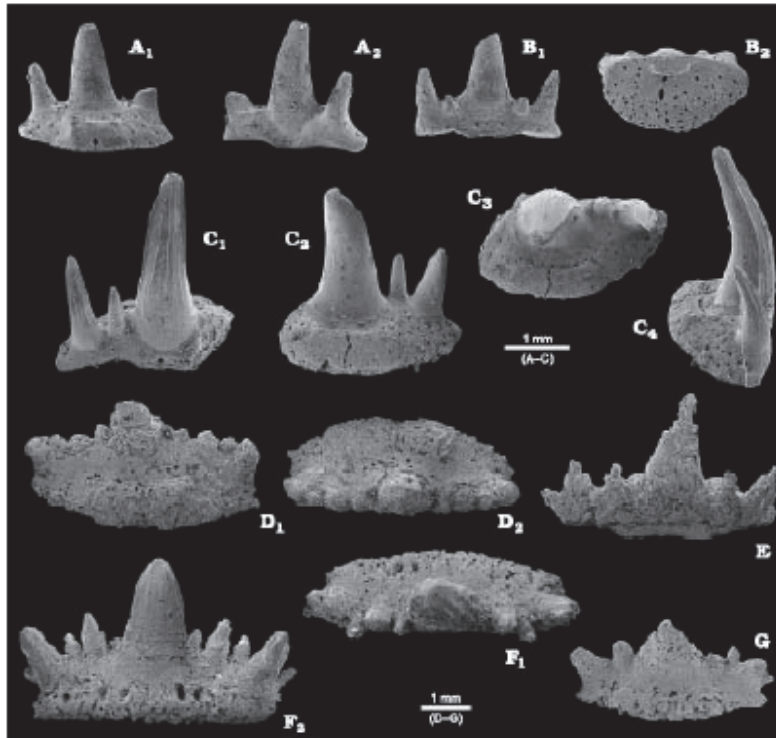


Figure 9. Different cladodont style teeth found in the Middle Tournaisian of Muhua, China in the Muhua Formation from Ginter et al., 2007.

## **Chapter 4: Materials and Methods**

At East Liberty, samples were collected from spoil piles. At Little Hardwick Creek, the bone bed could be accessed and samples were collected directly from it. At East Liberty, samples were taken from below the bone bed at the spoil pile by bringing back larger rocks that included bone bed at the top surface of the rock with limestone beneath bone bed. From the hand samples taken at each location, and from measuring sections of the exposure, a graphic sedimentary log was produced using Strater® (Golden Software Strater).

Once the samples were brought back to the lab, they were washed and scrubbed over US #40 and #60 sieves. The material that was washed off during the initial processing of the samples was dried and stored in containers until the material could be observed under a dissecting microscope. During the initial washing, all visible macroscopic vertebrate material was prepared out of the rock using pneumatics to chip away matrix surrounding vertebrate material so that the vertebrate material could be removed without extensive damage to the vertebrate material. Once the collected material was cleaned of soil, sediment, and loose vertebrate material, each portion was broken into pieces ranging from one to two centimeters in length and thickness. All material was then placed in stainless steel screen buckets and immersed into weak organic acid solutions (Jepperson et al., 1999).

Formic acid (20% and 15% buffered to pH 2.75) and acetic acid (20% and 15%) was used to break down the samples. The purpose of using two different types and concentrations of acids was to determine which acid and concentration was the most effective at producing the highest yield and, more importantly, determining which acid

did the least amount of acid etching to the vertebrate remains. Mass of initial yields were the same before being placed in the different acid concentrations. After breakdown of the rock, remaining residue was then measured to determine the greatest mass of material remaining. The acid that produced the greatest mass of remaining residue was then determined to be the best acid and concentration of acid to use to breakdown the rock.

After the acid treated material was dried, it was observed under a dissecting microscope for closer examination. Vertebrate material and conodonts were extracted from the material using tweezers and dissecting needles. The material extracted was sorted in categories; teeth, scales, conodonts and unknown material. For a closer examination of selected specimens, SEM photographs were obtained and analyzed. Based upon close examination of the specimens, identifications were performed using descriptions provided by various authors. Specimens were identified to the species level where possible.



## **CH. 5 East Liberty Bone Bed**

### **5.1 Introduction**

The East Liberty Bone-Bed is of great importance because it reveals some of the earliest gnathostome taxa. The bone-bed essentially forms the boundary between the oxygen rich waters of the Delaware Limestone and the oxygen depleted waters of the Olentangy Shale.

The East Liberty bone-bed is exposed within the Shelly Materials Quarry, located in Logan County, Ohio. The vertebrate/phosphate-rich bed most likely formed during a Highstand Systems Tract when net erosion and winnowing allowed for an accumulation of resistant materials. These resistant materials include phosphate pebbles, silt sized quartz grains and vertebrate material, including conodonts, placoderms, acanthodians and chondrichthyes.

The East Liberty Bone Bed was first defined by John Wells in 1944 (Wells, 1944). Wells described the geology of the East Liberty Quarry and a limited explanation of vertebrate material found with no explanation as to how the bone bed formed. Conkin and Conkin (1998) used Wells' findings to help describe paracontinuities but did not perform actual research at the quarry. Mann (2007) defined the stratigraphy and lithology of quarry, and described the conodont faunas of the Delaware Limestone and the Ohio and Olentangy Shales. While the stratigraphy, lithology, and conodont biostratigraphy have been analyzed, bone-bed formation, and the vertebrate faunal diversity and taxonomy have been largely ignored. A detailed analysis of the bone-bed and inclusive fauna is needed to gain insight on how vertebrate material accumulated forming a bone-

bed, as well as, to get an idea of the paleoecology of the epicontinental seas during the Devonian in central-west central Ohio.

## **5.2 Location**

The East Liberty bone-bed is well exposed within the Shelly Materials Quarry, located on OH SR 292 in Logan County, Ohio. The East Liberty Bone Bed can be found in East Liberty, Ohio (Fig. 10) (Fig.11).



Fig. 10. Satellite view of Shelly Materials quarry in East Liberty, Ohio. The yellow line indicates the exposed extent of the bone bed (Figure courtesy of google maps).

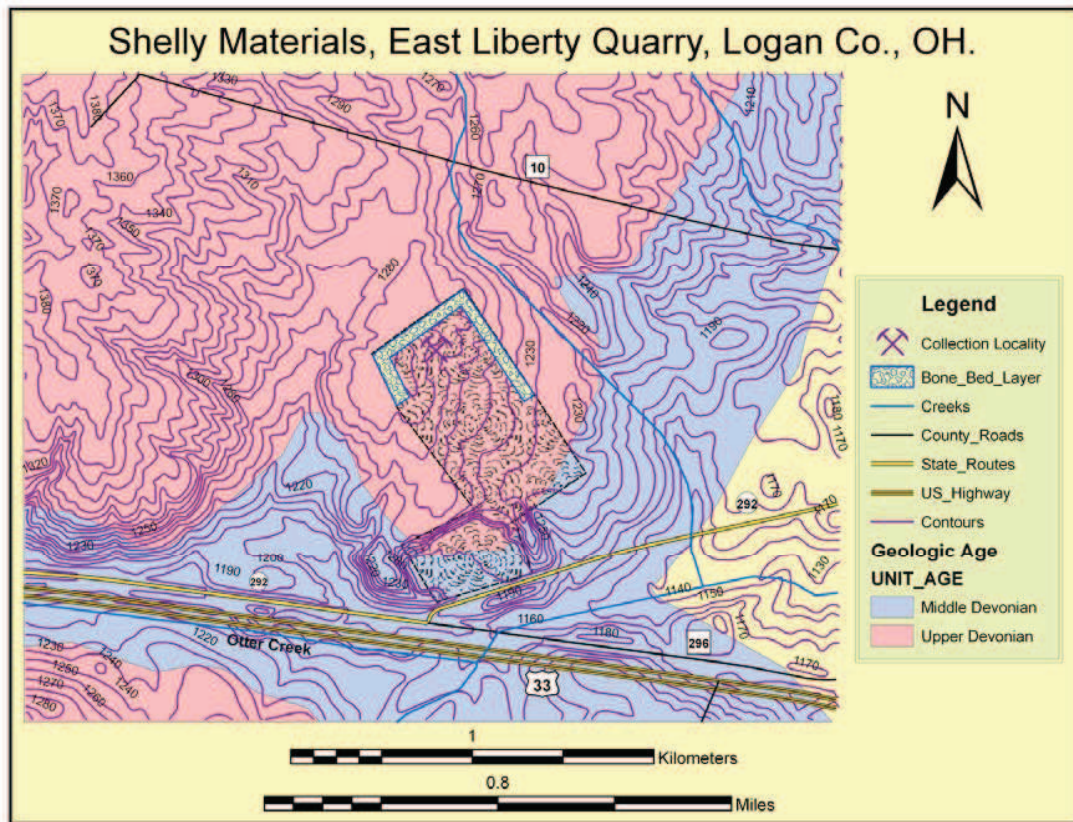


Figure 11. Aerial topographic map showing the East Liberty Quarry (C. Ciampaglio).

The vertebrate/phosphate-rich layer is located in the top tier/ledge of the quarry “high-wall.” The bone bed is located between the Olentangy Shale from above and the Delaware Limestone from below (Fig. 12) (Fig. 13).



Fig. 12. Photo showing the ledge at the East Liberty quarry where the bone bed can be found.

# East Liberty Bone Bed

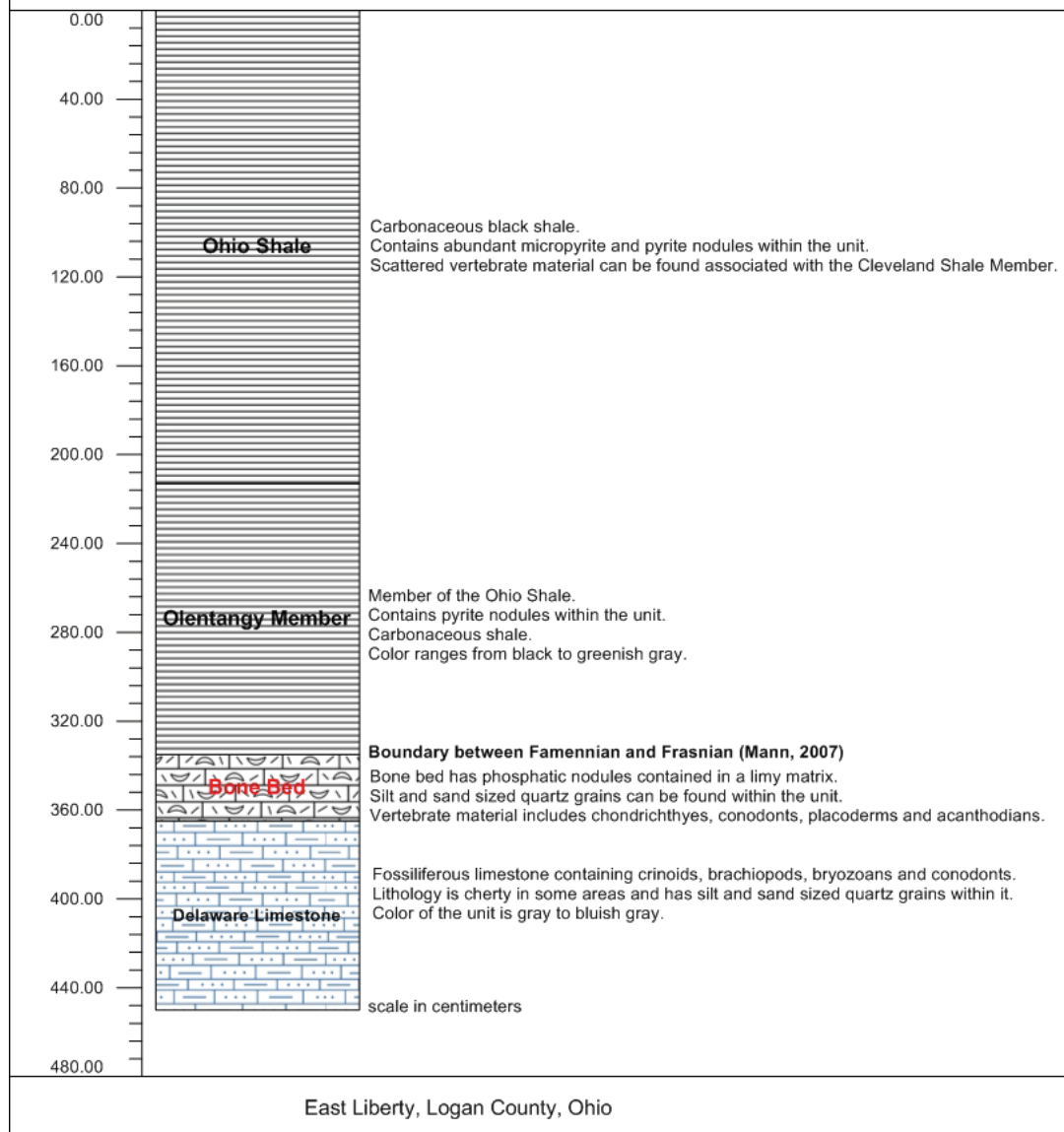


Fig. 13. Graphic sedimentary log of the East Liberty quarry.

### 5.3 Formation of Bone Bed

The East Liberty Bone-Bed lies at the interface of the Delaware Limestone and the Olentangy Shale. Since the bone-bed marks an unconformity, presumably the erosion weathered materials below the bone bed, and winnowing left behind more durable material; bone, teeth, scales, denticles and phosphate material. The material would have initially been deposited on a carbonate shelf environment while sea level was of moderate depths. This allowed resistant material to be accumulated with other nonresistant material.

The East Liberty bone bed is sandwiched between a carbonate shelf environment and a basin environment. The resistant material is thought to have accumulated on a shelf like environment at first, and then later brought out to a basin environment from a transgressive sequence. This suggests that during the onward advancement of shoreline, the waves eroded the less resistant material, carbonates, and left behind the more durable material in winnowed pockets which then formed lag concentrations of vertebrate material.

### 5.4 Systematics

#### 5.4.1 Class Conodonta

Order Ozarkodinida Dzik, 1976

Family Spathognathodontidae Hess, 1959

Genus *Ancyrodella* Ulrich and Bassler, 1926

*Ancyrodella buckeyensis* Stauffer, 1938



The Pa element had a secondary carina which terminated at the main carina.

#### **5.4.2 Class Placodermi**

**Class: Placodermi**

**Order: Arthrodira**

Placoderm material consisted of undifferentiated plates. Disarticulated plates could be observed on the surface of the bone bed, all belonging to arthrodiras.

#### **5.4.3 Class Chondrichthyes**

Subclass Chondrichthyes

Infraclass Elasmobranchii

Order Euselachii Hay 1902

Superfamily Protacrodontidea nov.

*Protacrodus* Jaekal 1921

*Protacrodus vestustus* Jaekal 1921

*Protacrodus* teeth were observed with less frequently as cladodont teeth in the East Liberty Bone Bed. All *Protacrodus* sp. were identified by their unique design of their primary and secondary, or lateral cusps. Each cusp has a bifurcating ridges descending from their tip. The central cusp is larger in height than the lateral cusps flanking it on either side. Figures 1, and 2, of Plate I show specimens of *Protacrodus vestustus* Jaekal 1921 (Gross, 1973; Zangerl, 1981; Turner, 1982; Lelievre and Derycke, 1998; Ginter, 2002; Duncan, 2006) in various profiles. The specimen shown in Figure 1

measures 1.4 mm long along the full length of the tooth. Ridge detail is especially visible on Figure 1. The specimen shown in Figure 2 measures 2.28 mm long along the length of the tooth, and not only shows ridge detail, but also reveals the disparity between the heights of the cusps, with the medial cusp height being larger than that of the flanking lateral cusps.

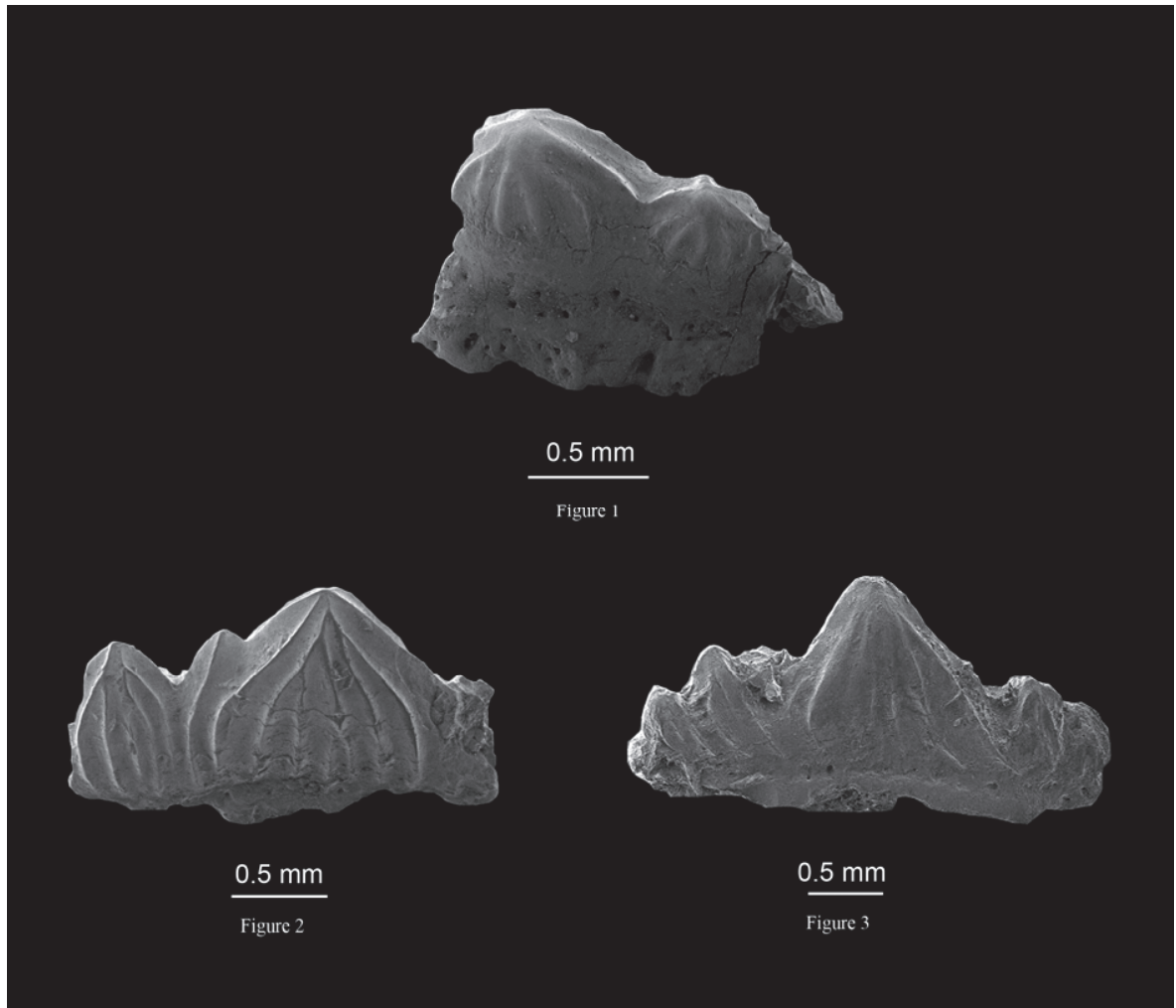


Plate I. *Protacrodus vestustus* specimens found in the East Liberty bone bed. Figs. 1-3.

*Protacrodus vestustus* (Jaekal). 1, sample 2-2-1, labial; x50. 2, sample 2-8-1, labial; x25.

3, sample 1-9-1, lingual; x50.

All specimens were collected from the East Liberty bone bed in East Liberty, Ohio, as described by Mann et al., 2007.

Subclass Chondrichthyes

Infraclass Elasmobranchii

Order Euselachii Hay 1902

Family Phoebodontidae Williams 1979

*Phoebodus* ST John and Worthen 1875A

*Phoebodus poliatus* Newberry

Recognition of *Phoebodus* sp. was determined by the cladodont style of teeth, where the central cusp is no longer than the lateral cusps. Furthermore, phoebodont teeth have cusps that are tilted away from the central cusp at angles of 30° to 40°. Figures 1- 4, of Plate II, show specimens of *Protacrodus poliatus* Newberry (Gross, 1973). The specimen, shown in Figure 1 measures 1.3 mm long along the length of the tooth, in lingual view. The specimen shown in Figure 1 clearly illustrates that the lateral cusp is tilted about 40° from the central cusp. In Figure 2 (Plate II) the tooth measures 1.4 mm long along the length of the tooth, in lingual view. The specimen in Figure 3 measures 1.1 mm long along the length of the tooth, in lingual-occlusal view. The lateral cusps are tilted away from the central cusp. Figure 4 measures 1.6 mm long along the length of the tooth, in lingual view. The specimen shown in Figure 4 clearly illustrates the tilting of the lateral cusps away from the central cusp (Gross, 1973).

Figure 5 is a specimen of cladodont tooth-style, but exact placement of the tooth within genus, whether that of phoebodontid or the stethacanthid is uncertain. The lateral cusps are tilted away from the central cusp similar to that of the phoebodontids, but the lateral cusps are no greater in size than the central cusp as in stethacanthids. This tooth is a lingual-occlusal view that measures 1.5 mm long along the length of the tooth.

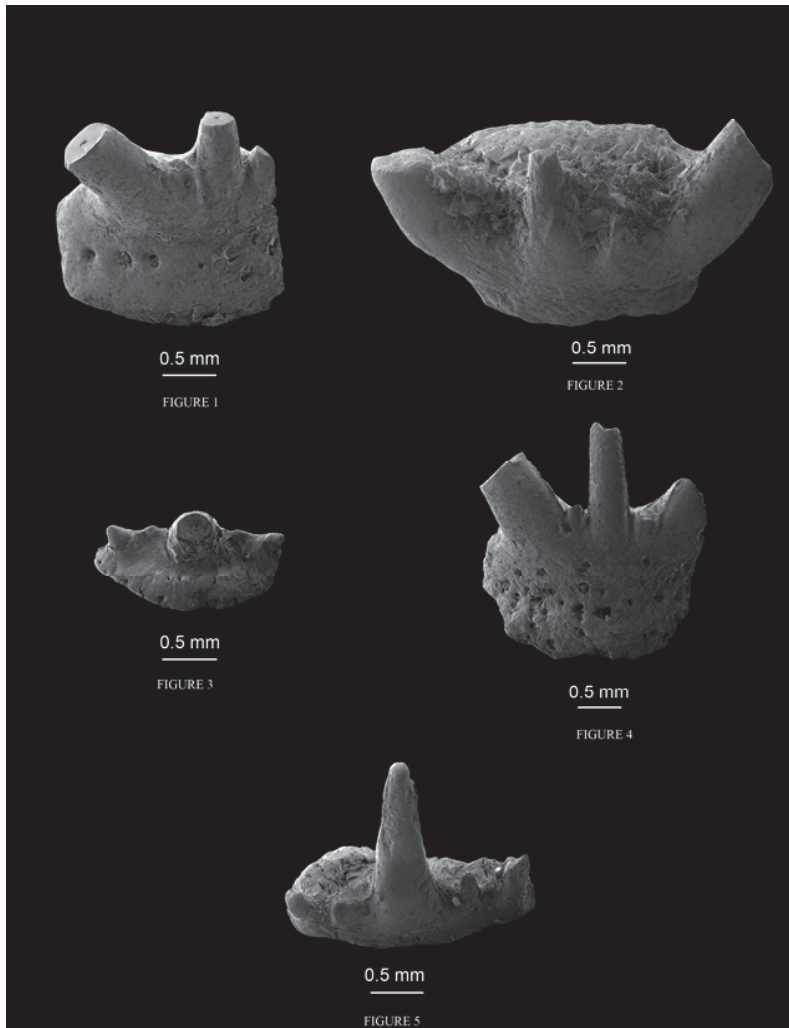


Plate II. Different cladodont teeth found in the East Liberty bone bed. Figs. 1-4.

*Phoebodus poliatus* (Newberry). 1, sample 2-4-1, lingual-occlusal; x50. 2, sample 4-6-2, occlusal; x45. 3, sample 2-5-1, lingual-occlusal; x50. 4, sample 2-10-1, lingual; x40. Fig. 5. Cladodont Style. Sample 4-4-1, lingual-occlusal; x50.

All specimens were collected from the East Liberty bone bed in East Liberty, Ohio, as described by Mann et. al., 2007.

## 5.5 Discussion

The East Liberty Bone Bed produced good amounts of microvertebrate material. The best way to recover the material was through the use of a buffered formic acid solution. From the different acid techniques described above, the buffered formic acid solution produced the highest yield per a determined sample weight.

The bone bed was found at the boundary between the Deleware Limestone and the Olentangy Shale. Exact determination of the age of the bone bed is unspecified because the lack of clear indicative conodont biozones. Observed were Late Frasnian conodonts represented by *Ancryodella beckeensis*, *A. curvata* and *Ancyrognathus asymmetricus*. From these mixtures of conodonts, the East Liberty Bone Bed falls at the boundary of the Late Frasnian and Early Famennian, thus representing a boundary between the Frasnian and Famennian.

There are several proposed theories as to how marine bone beds form, isolation of sediment allowing it to accumulate, filling in a groove created by some mechanical tool and through erosion of material leaving behind more durable sediments and vertebrate ichthyoliths. I have proposed that the East Liberty Bone Bed has formed through net erosion since there is a mixture of conodonts from the Late Frasnian and earlier Frasnian conodonts, thus meaning an erosional event occurred for that mixture to accumulate. Furthermore, the bone bed is almost completely devoid of less resistant material, such as calcite. The bone bed contains silty to sandy quartz grains, traces of pyrite, phosphate pebbles and vertebrate material, all of which are durable to erosional events. Moreover, the condition of the vertebrate material showed weathering had taken place on the material. The material more often than not was broken and fragmented. Whole vertebrate

ichthyoliths were rarely seen. However, the condition of the vertebrate material could have been damaged through acid etching and/or breaking of the rock; therefore, it should not be the only factor used for determination of a net erosional bone bed. Considering other factors, mixture of Givetian and Frasnian conodonts, accumulation of durable material, as well as fragmentation of vertebrate ichthyolith all indicate that the bone bed was produced from net erosional events.

The East Liberty Bone Bed was exceptionally rich in vertebrate material. Phoeodontid material was found with the greatest significance, with decreased abundances of *Protacrodus* and possibly undeterminable *Stethacanthus* and *Symmorium* teeth remains due to fragmentation of the lateral cusps. Phoeodontids, Protacrodontids and Cladoselachids all are shallow water fauna. Remains are commonly associated with high energy, well oxygenated, shallow shelves. This suggests that the East Liberty Bone Bed accumulated material in such an environment, shallow marine shelf.

Chondrichthyan remains were all fairly young in the evolution of the chondrichthyans. The East Liberty Bone Bed gives a glimpse into the early evolution of chondrichthyans. All of the species discovered still have primitive traits associated with them linking them back to their ancestral past.

## **Ch. 6: Little Hardwick Creek Bone Bed**

### **6.1 Introduction**

Little Hardwick Creek Bone Bed was identified by Brett et al. (2003) and was divided into three different sections: A, B and C, with A being the oldest of the three. Bone Bed C was collected and analyzed for this particular study. The purpose of collecting Bone Bed C in this study was to observe the chondrichthyan fauna, as well as to observe the conodonts and which conodont biozone they belonged to.

### **6.2 Location**

Little Hardwick Creek Bone Bed is located in Vaughn's Mill, Kentucky. Access to bone bed is along Townsend Road (Fig. 14).





Fig. 14. Aerial view of the location of Little Hardwick Creek bone bed. Arrow depicts approximate location of bone bed C found in Little Hardwick Creek in Vaughn's Mill, KY (Google Maps).

The bone bed can be found in the creek bed as it juts out from the creek wall. Three different bone beds can be found at this location as described by Brett et al. (bone beds A, B and C). For this study Bone Bed C was analyzed and found from the description given by Brett et al. (Fig. 15) (Brett et al., 2003).

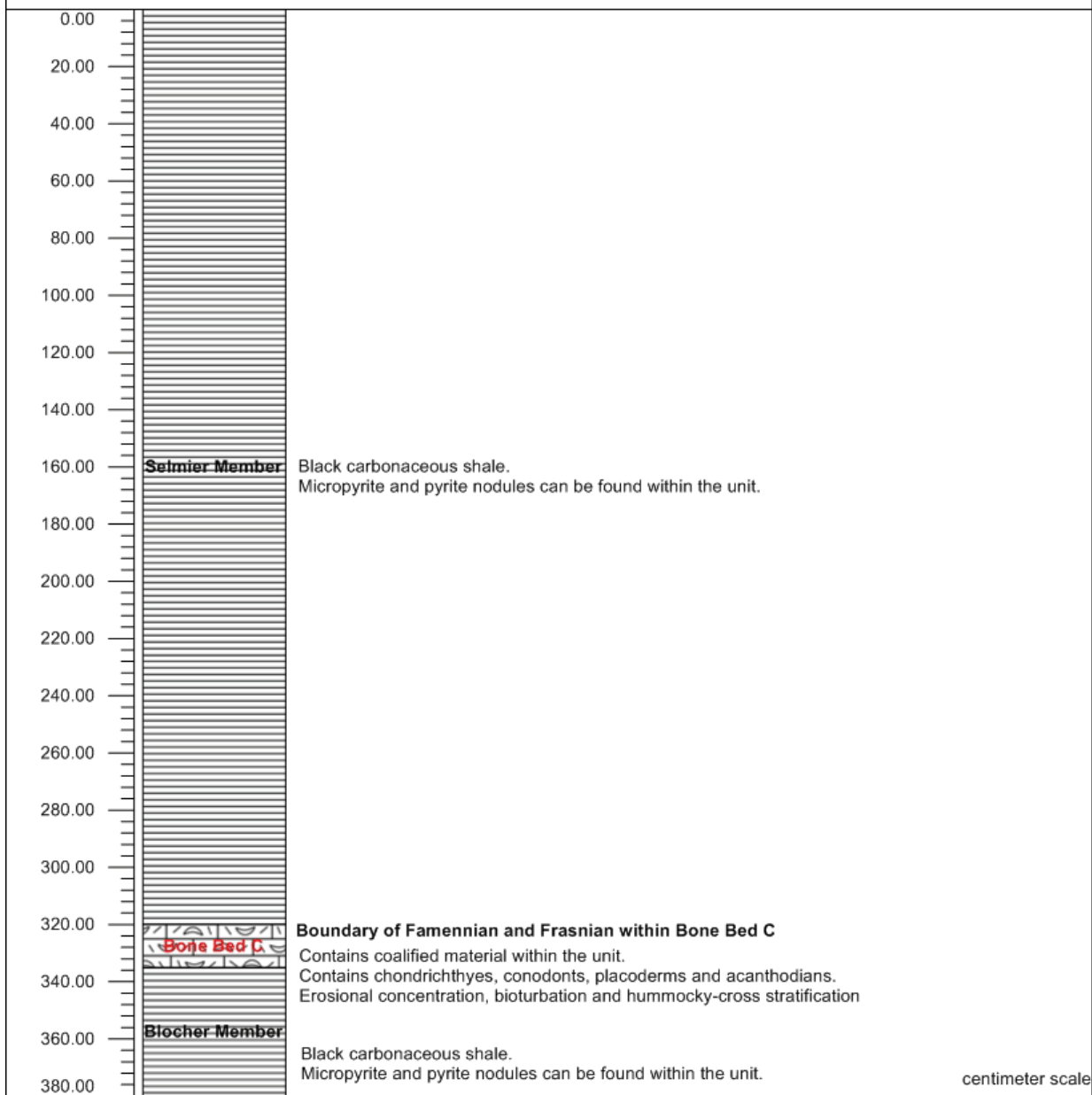


Fig. 15. Little Hardwick Creek. Arrow depicts where samples were collected.

### **6.3 Formation of Bone Bed**

Bone Bed C ranges in thickness from 0.5-5 cm. Bone Bed C can be divided into an upper and lower layer. The lower layer has hummocky cross stratification, thus the lower portion is a storm deposit. The upper portion formed by a continuous cycle of deposition and erosion. The erosion of the material left behind more durable material, such as phosphate material, bone and teeth in a thin concentrated layer (Brett et al., 2003). Bone Bed C is Famennian in age, determined by well-preserved conodonts that are applicable to conodont biostratigraphy. Stratigraphically, Bone Bed C is wedged between the Olentangy Formation, below, and the Huron Formation above, where Bone Bed C actually marks the base of the Lower Huron Formation (Fig. 16) (Brett et al., 2003; Rogers et al., 2007).

# Little Hardwick Creek Bone Bed C



Vaughn's Mill, Kentucky

Fig. 16. Graphic sedimentary log of Little Hardwick Creek in Vaughns Mill, KY (Strater®).

## **6.4 Systematics**

### **6.4.1 Class Conodonta**

Class Conodonta

Order Polygnathacea

Family Polygnathidae Bassler 1925

*Palmatolepis* Ulrich and Bassler, 1926

*Palmatolepis* sp. have multimembrate assemblages with ramiform and pectiniform but no coniform elements (Clark et al., 1981). Figures 1-3, Plate III are *Palmatolepis triangularis* Sanneman (Clark and Ethington, 1967; Ji et al., 1992). All three of these figures show the upper surface. All specimens have thin, broad plates with a wide lateral lobe. Figures 4-6 show specimens of *Palmatolepis subperlobata* Branson and Mehl (Clark and Ethington, 1967). Figures 4-6 are all upper surface views.

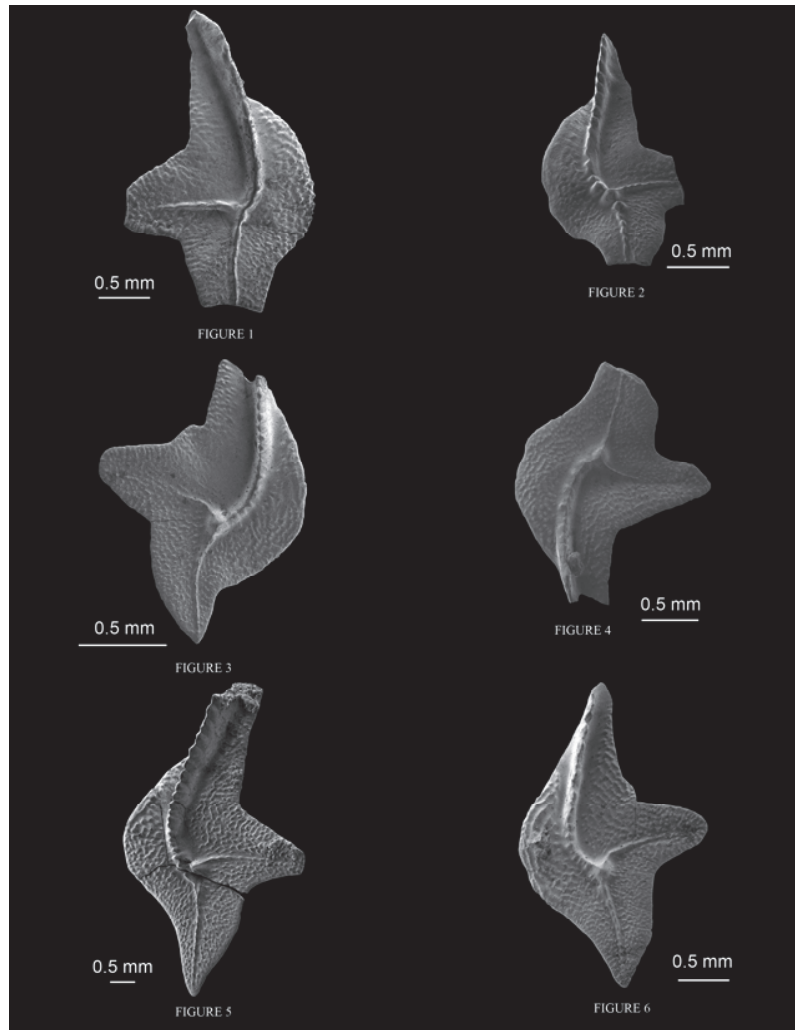


Plate III. Different *Palmatolepis* sp. found in Little Hardwick Creek Bone Bed C. Figs. 1-3. *Palmatolepis triangularis*. 1, sample 1-17-1, P<sub>1</sub> (Pa) element, upper surface; x50. 2, sample 2-14-1, P<sub>1</sub> (Pa) element, upper surface; x50. 3, sample 3-2-1, P<sub>1</sub> (Pa) element, upper surface; x50. Figs. 4-6. *Palmatolepis subperlobata* (Branson & Mehl). 4, sample 2-15-1, P<sub>1</sub> (Pa) element, upper surface; x50. 5, sample 3-4-1, P<sub>1</sub> (Pa) element, upper surface; x50. 6, sample 3-16-1, P<sub>1</sub> (Pa) element, upper surface; x40.

All specimens were collected from Bone Bed C at Little Hardwick Creek in Vaughns Mill, Kentucky, as described by Brett et. al., 2003.

*Ancryodella* Ulrich and Bassler 1926

*Ancryodella rotundiloba* Bryant

Figures 1 and 3, Plate IV shows specimens that belong to *Ancryodella rotundiloba* Bryant (Clark and Ethington, 1967; Ji et al., 1992). Pectiniform in morphology, *A. rotundiloba* often portrays segments of their ornamentation with evidence of resorption and subsequent regeneration. The function of this resorption and regeneration is thought to be for either for protection or repair. Pits can be observed on the surface of these specimens which are used as muscle attachment sites. *A. rotundiloba* preferred slightly deep waters (Clark et al., 1981).

Class Conodonta

Order Polygnathacea

Family Polygnathidae Bassler 1925

*Ozarkodina* Branson and Mehl 1933

Figures 2, 5 and 7, Plate IV show Pa elements as either carminate or carminiscaphate. The Sa element is alate and lacking any posterior processes. *Ozarkodina* sp. have multimembrate assemblages with ramiform and pectiniform but no coniform elements (Clark et al., 1981).

Class Conodonta

Order Conodontophorida

Superfamily Prioniodontacea Bassler 1925

Family Icriodontidae Muller and Muller 1957

*Icriodus* Branson and Mehl

*Icriodus expansus* Branson and Mehl



Figures 4 and 6, Plate IV show *I. expansus* Branson and Mehl (Clark and Ethington, 1967). *Icriodus* sp. have trimembrate apparatuses including scaphate Pa elements, Pb and S elements. Pa elements of *Icriodus* Branson and Mehl typically have three rows of longitudinal rows (Clark et al., 1981).

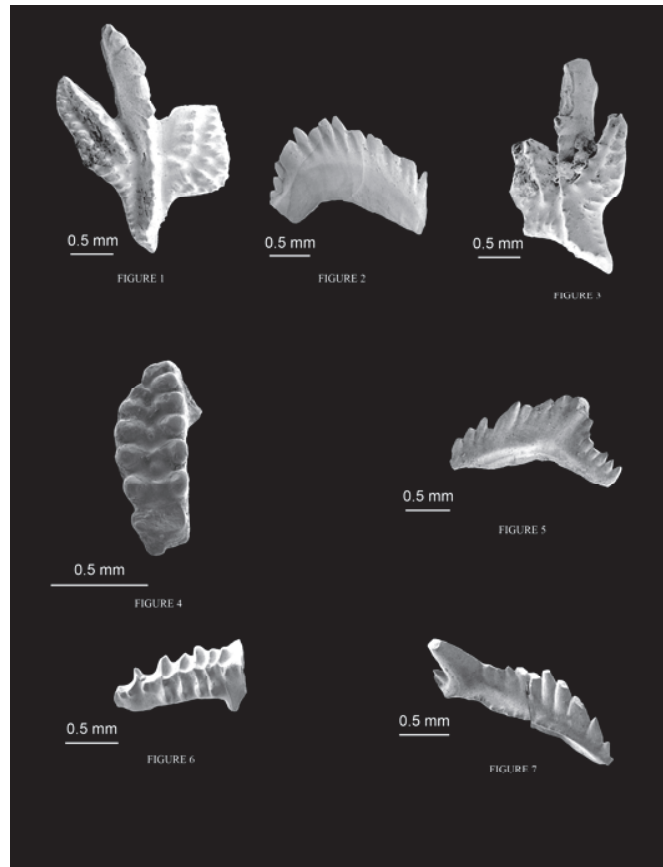


Plate IV. Different conodont specimens found in Little Hardwick Creek Bone Bed C.

Figs. 1 and 3. *Ancyrodella rotundiloba* Bryant. 1, sample 1-18-1, P<sub>1</sub> (Pa) element, upper surface; x50. 3, sample 3-1-1, P<sub>1</sub> (Pa) element, upper surface; x40. Fig. 2, 5 and 7.

*Ozarkodina* Branson & Mehl 1933. 2, sample 2-16-1, Pa element, lateral; x50. 5, sample 3-8-1, Pa element, lateral; x50. 5, sample 3-17-1, Pa element, lateral; x50, 7, sample 3-19-1, Pa element, lateral; x50. Figs. 4-6. *Icriodus expansus* Branson & Mehl. 4, sample 3-3-2, Pa element, upper surface; x100. 6, sample 3-15-1, Pa element, upper surface; x50.

All specimens were collected from Bone Bed C at Little Hardwick Creek in Vaughns Mill, Kentucky, as described by Brett et. al., 2003.

#### 6.4.2 Class Placodermi

Subclass Placodermi

Suborder Rhenanida

Family Asterosteidae

*Ohioaspis*

*Ohioaspis tumulosus* Wells 1944

First identified by Wells (Wells, 1944), these placoderm scales are buchanosteid-type body scales (Gross, 1973; Turner and Murphy, 1988).

#### 6.4.3 Class Chondrichthyes

Subclass Chondrichthyes

Infraclass Elasmobranchii

Order Euselachii Hay 1902

Superfamily Protacrodontidea nov.

*Protacrodus* Jaekal 1921

*Protacrodus* teeth were identified based upon their unique design with the lateral modified cusps. The rounded lateral cusps have bifurcating ridges descending from their tips of their cusps. The central cusp is of the same design as the lateral cusps but larger. Figures 3-5, Plate V show *Protacrodus* teeth. Figure 3 is of an occlusal view, which shows the central cusp, as well as two lateral cusps. Figure 4 is a lingual view, that shows a central cusp and less defined lateral cusps. Figure 5 is of a lingual view that shows the

central cusp and one lateral cusp (Gross, 1973; Zangerl, 1981; Turner, 1982; Lelievre and Derycke, 1998; Ginter, 2002; Duncan, 2006).

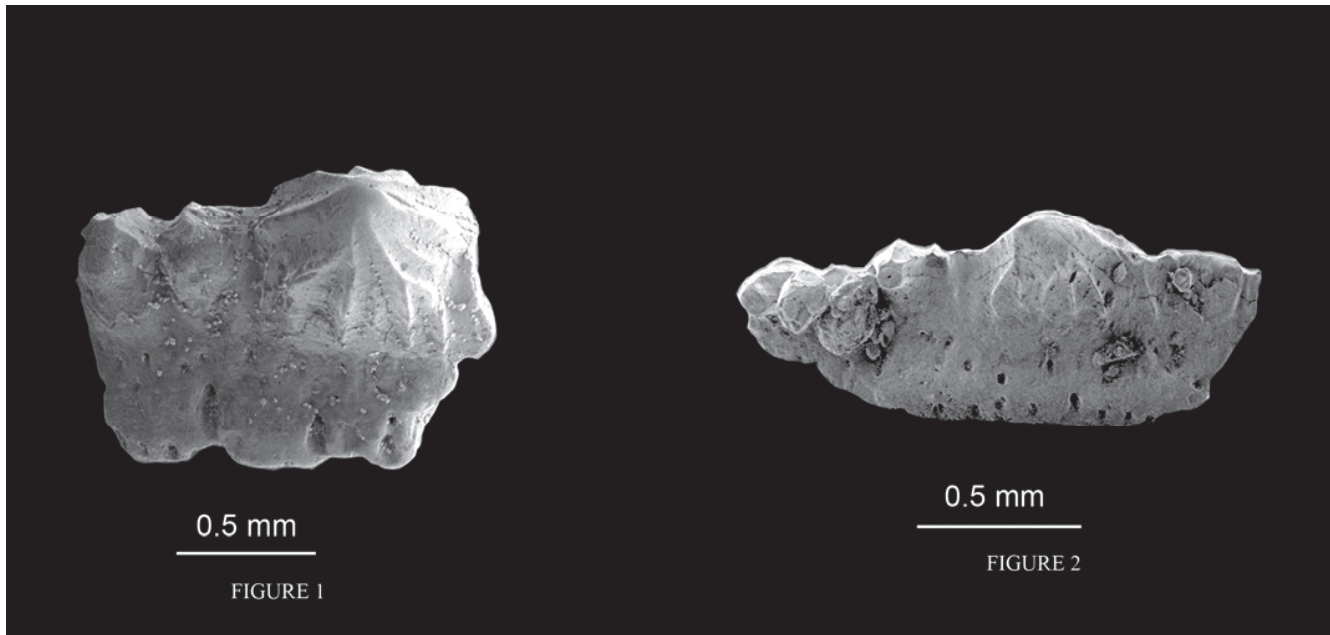


Plate V. *Protacrodus* sp. found in Little Hardwick Creek Bone Bed C. Figs. 1-2.

*Protacrodus* sp. 1, sample 1-5-1, occlusal; x50. 2, sample 1-6-2, lingual; x50. 3, sample 1-9-1, lingual; x50.

All specimens were collected from Bone Bed C at Little Hardwick Creek in Vaughns Mill, Kentucky, as described by Brett et al., 2003.

Family Cladoselachidae

*Ohiolepis* Wells 1944

*Ohiolepis newberryi* Wells 1944

Figures 5-6, Plate VI were identified using Wells (1944) and Gross (1973). The only remains to have been found of *Ohiolepis* are those of dermal denticles. The denticles have flattened tubercles that cover its superior surface. Other chondrichthyan dermal denticles were observed but not identified to the genus level, figures 1-4.

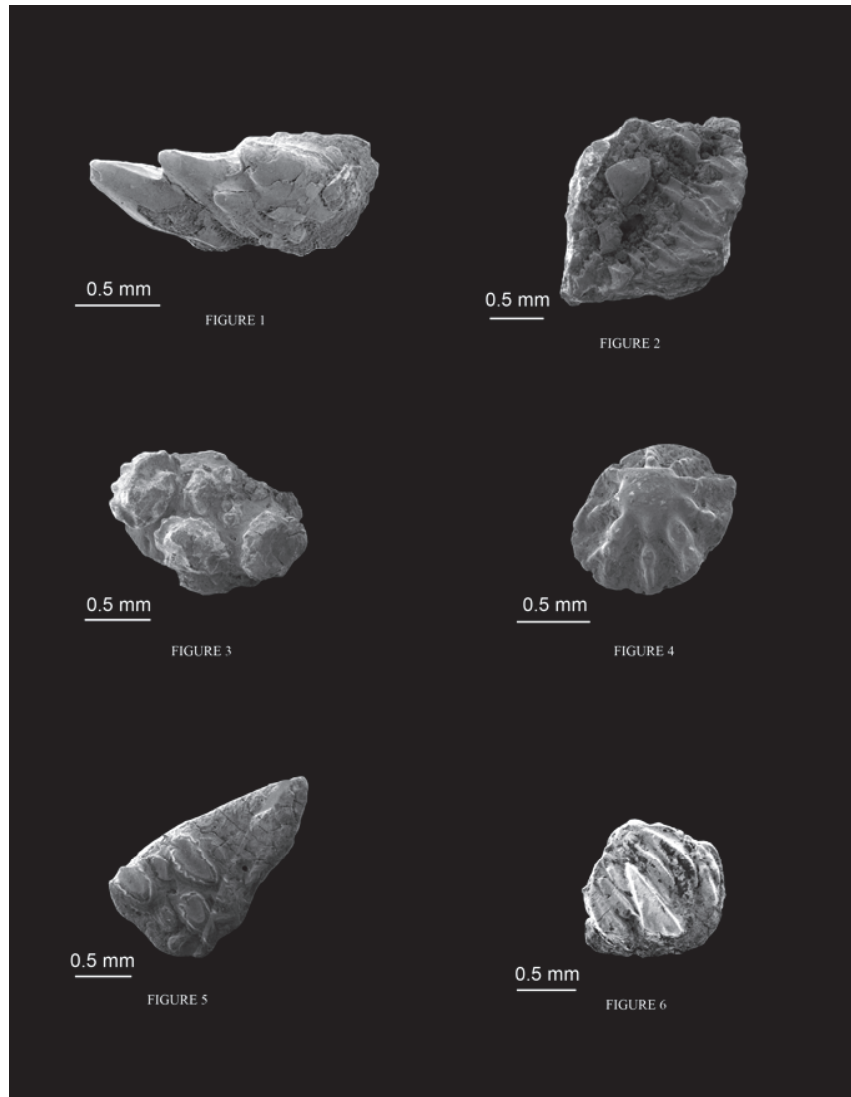


Plate VI. Chondrichthyan dermal denticles found in Little Hardwick Creek Bone Bed C.

Figs. 1-4. Chondrichthyan Dermal Denticles. 1, sample 1-1-1, occlusal; x50. 2, sample 1-4-1, occlusal; x50. 3, sample 1-10-1, occlusal; x50, 4, sample, 1-7-1, occlusal; x65.

Figs. 5-6. *Ohiolepis newberryi* (Wells). 5, sample 3-5-1, occlusal; x50. 6, sample 3-14-1, occlusal; x50.

All specimens were collected from Bone Bed C at Little Hardwick Creek in Vaughns Mill, Kentucky, as described by Brett et al., 2003.

Family Phoebodontidae Williams 1979

*Phoebodus* ST John and Worthen 1875A

*Phoebodus poliatus* Newberry

*Phoebodus poliatus* Newberry was determined by analyzing the tilt of the lateral cusps from the central cusp, and upon whether or not the central cusp was no longer than the lateral cusps. Figure 1, Plate VII shows a specimen of *Phoebodus poliatus* Newberry (Gross, 1973). Specimens show in Figures 2-3, Plate VII could not be differentiated as to whether they belonged to the genus *Stethacanthus* or *Phoebodus*, so they are labeled as cladodont style teeth. Figure 2 does not have clear lateral cusps to determine what, if any, tilt the lateral cusps were in reference to the central cusp. Figure 3 does not have pronounced lateral cusps; although, the lateral cusps that are present are tilted away from the central cusp.



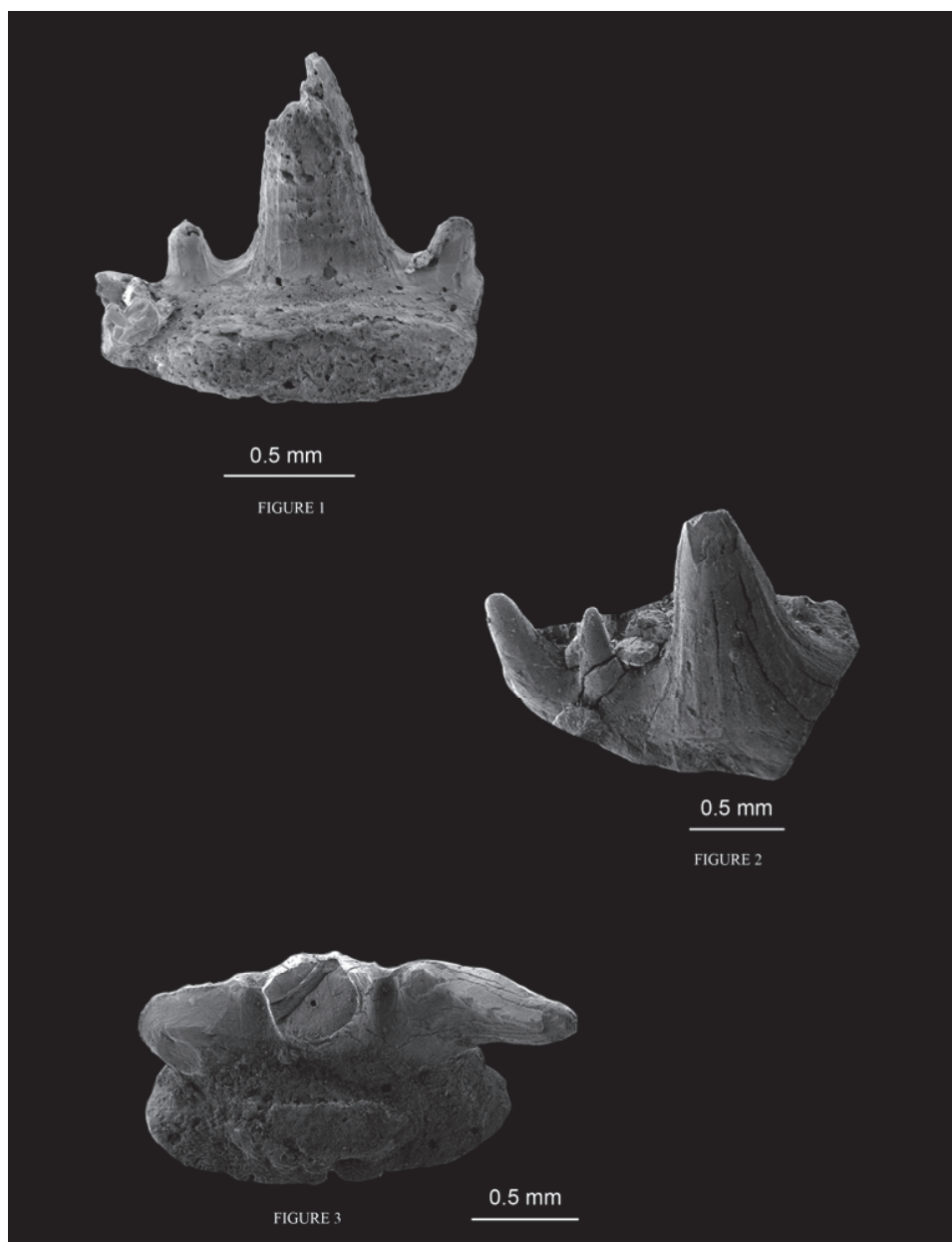


Plate VII. Different cladodont teeth found in Little Hardwick Creek Bone Bed C.

Fig. 1. *Phoebodus poliatus* (Newberry). Sample 1-11-1, labial; x50. Figs. 2-3. Cladodont Teeth. 2, sample 1-12-3, lingual; x70. 3, sample 1-2-1, labial; x50.

All specimens were collected from Bone Bed C at Little Hardwick Creek in Vaughns Mill, Kentucky, as described by Brett et al., 2003.

## **6.5 Discussion**

Little Hardwick Creek Bone Bed C formed through a net negative accumulation of sediment which allowed the more persistent material to be left behind, including phosphatic pebbles and vertebrate material. The Little Hardwick Bone Bed ranges in thickness from 0.5-5.0 cm.

The vertebrate material found within the Little Hardwick Bone Bed consisted of conodonts, chondrichthyans and acanthodians. The conodonts were well preserved and identifiable leaving to the opportunity of placing them in an established conodont biozone.

## **Ch. 7: Comparison of East Liberty Bone Bed and Little Hardwick Bone Bed**

### **7.1 Introduction**

Both East Liberty Bone Bed and Little Hardwick Creek Bone Bed C formed through similar processes. The contents of both beds are of a durable nature, as well as a mixture of conodonts lend evidence to the beds being formed through a net loss erosion process.

East Liberty Bone Bed marks the boundary between the Frasnian and Famennian at East Liberty. Little Hardwick Creek Bone Bed C marks the boundary between the Blocher and Selmier Members at Little Hardwick Creek. The mixture of conodonts negates the possibility of assigning each bone bed an exact conodont biozone, but rather allows for the determination of an age range of the bone beds. Faunas for both locations are rich and diverse. While the faunas are similar, there are key differences between the two with the conodont fauna.

### **7.2 Bone Bed Comparison**

East Liberty Bone Bed is enriched in silt-sized quartz grains, phosphate pebbles and vertebrate material. Quartz makes up about one-third of the remaining sediment, phosphate pebbles comprise approximately sixty percent and vertebrate material consists of about, for approximately seven percent. The lithological portion is composed of dolomite, phosphate pebbles, quartz and vertebrate material, void of soft durable material. The soft and less durable material was eroded away, leaving behind a dense, concentrated bed of durable material. Little Hardwick Creek Bone Bed C is comprised of

silt sized quartz grains, phosphate pebbles and vertebrate material. Quartz makes up about twenty percent of the remaining sediment, phosphate pebbles comprise approximately sixty-five percent and vertebrate material approximately comprises fifteen percent of the remaining sediment. Much like East Liberty Bone Bed, the lithological portion at Little Hardwick Creek is composed of dolomite, quartz, phosphate pebbles and vertebrate material. This concentrated layer of durable, vertebrate rich material was formed through erosion.

Conodonts, fish and chondrichthyan remains were found at both the East Liberty Bone Bed and Little Hardwick Creek Bone Bed C. Isolated conodonts were all fairly well preserved. The mixtures of conodont faunas, at both locations, suggest some type of erosion, with older units mixing with younger units. Fish and chondrichthyan remains were not preserved as well as conodonts. The fish and chondrichthyan material at East Liberty Bone Bed were more fragmented and less numerous than that of Little Hardwick Creek Bone Bed C. They could be more fragmented due to acid etching, which would be entirely separate from depositional conditions. Less numerous remains could be the result, from the lack of original lithological material, acid etching, or loss during erosion.

Brett et al. (2003) determined Bed C at Little Hardwick Creek had hummocky cross stratification and a fining upward sequence in the layer. During storms, the wave base was lowered and the storm waves were able to sweep the sediments out into the basin where the more dense material settled out of suspension first, thus creating the fining upwards trends noted. East Liberty Bone Bed formed through transgressive events when waves created a winnowing effect where the more durable, dense material was able to fill voids and create a lag concentration of vertebrate material. Each bone bed

experienced a mixing of conodont faunas from distinct biozones indicating that these layers mark an erosive boundary. This erosive boundary was due to physical eroding events, such as storms and waves.

The preferential preservation of resistant material, mixing of conodont faunas from distinct biozones and the state of preservation of conodonts, fish and chondrichthyan remains all point to erosive processes. Erosion would cause the breakdown of less durable material and/or sweep it out to deeper waters leaving behind a resistant, durable, thin concentrated layer. This would allow for resistant material to accumulate, compact and lithify. Both East Liberty Bone Bed and Little Hardwick Creek Bone Bed C formed through erosional-depositional processes with a net loss of material.

### **7.3 Conodont Biozone Comparison**

Mann et al. (2007) analyzed conodonts from East Liberty Bone Bed and found a mixture of Late Frasnian and Givetian conodonts. Mann et al. suggest that East Liberty Bone Bed is a marker for the boundary between the Frasnian and Famennian.

Conodonts analyzed within this study included genera from both the Late Frasnian and Famennian as well. Late Frasnian conodonts were represented by *Ancyrodella buckeyensis*, *A. curvata* and *Ancyrognathus asymmetricus*. Famennian conodonts were represented by *Palmatolepis triangularis* and *P. subperlobata*, thus indicating a mixture of Late Frasnian and Famennian conodonts. As Mann et al. suggested, it appears that East Liberty Bone Bed is a definitive boundary marker bed for the Late Frasnian and Famennian.

Brett et al. (2003) analyzed conodonts from Little Hardwick Creek Bone Bed C and found a mixture of both Frasnian and Famennian conodonts. According to Brett et al., Bone Bed C at Little Hardwick Creek can be no younger than Upper *Crepida* Zone.

Conodonts analyzed in this study from Little Hardwick Creek Bone Bed C included representatives from both the Frasnian and Famennian. Frasnian conodonts were represented by *Ancyrodella rotundiloba*, *Ozarkodina macra*, *O. immersa*, *O. excavata* and *Icriodus expansus*. Famennian conodonts were represented by *Palmatolepis triangularis* and *Palmatolepis subperlobata*. *P. subperlobata* restricts Little Hardwick Creek Bone Bed C falls within the *triangularis* conodont biozone, approximately 374-376 ma. Little Hardwick Creek Bone Bed C falls between the underlying Blocher Member and the overlying Selmier Member (Fig. 17).

Correlation diagram for the highwall at Shelly Materials quarry in East Liberty, Ohio and the Little Hardwick Creek outcrop in Vaughn's Mill, Kentucky. The bone bed at East Liberty is lacking Famennian conodonts, whereas, bone bed C at Little Hardwick Creek contains Famennian conodonts, thus making the bed younger in age than the bone bed at East Liberty.

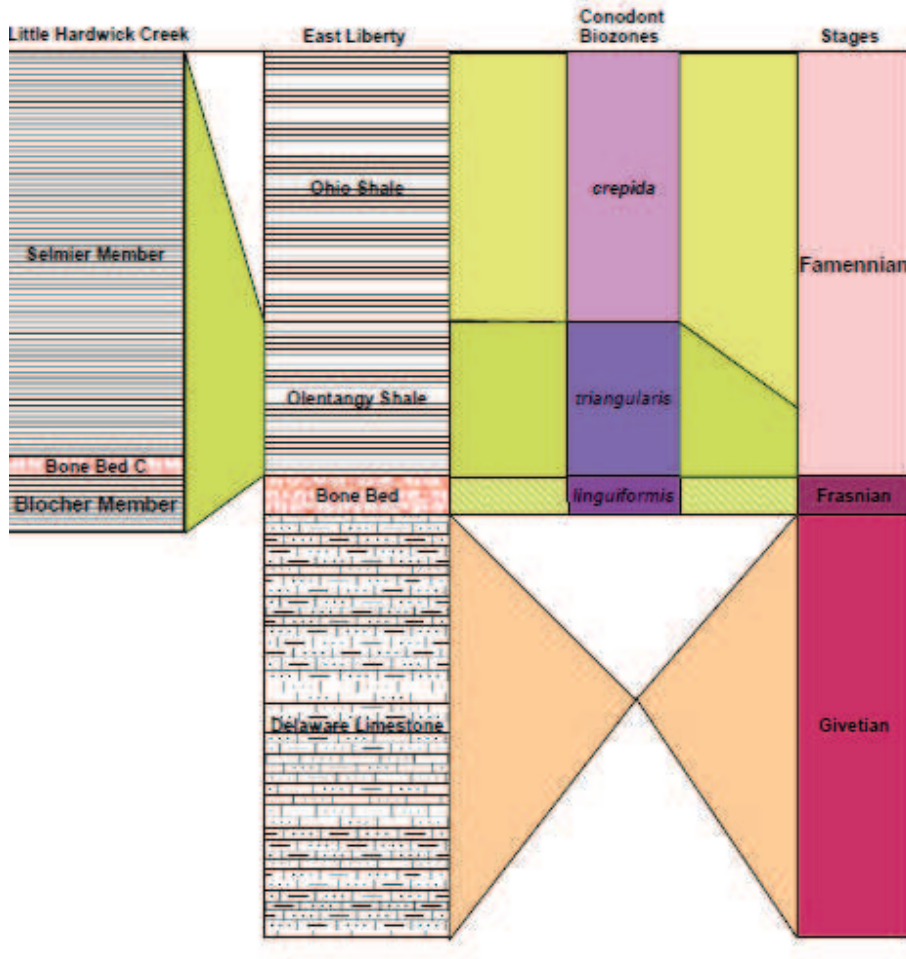


Figure 17. Correlation log between the East Liberty Bone Bed and the Little Hardwick Creek Bone Bed C.

#### **7.4 Faunal Comparison**

The faunas of East Liberty Bone Bed and Little Hardwick Creek Bone Bed C are typical of Late-Middle Devonian marine vertebrate biotas. Both faunas were dominated by acanthodian material. Anecdotally, acanthodians were found in more numerous amounts than placoderms or chondrichthyans.

A Sørensen Similarity Index was applied to compare East Liberty Bone Bed against Little Hardwick Creek Bone Bed C. The Sørensen Similarity Index provides a statistical evaluation of the relatedness between the two sites in terms of faunal composition. Omitting conodonts, a species count was performed for each location and the Sørensen similarity index was calculated. The results showed that the composition of the two sites were statistically identical, having a value of one.

#### **7.5 Conclusion**

East Liberty and Little Hardwick Creek were initially chosen for a study based on observation of the placement of the bone beds. Both layers appeared to mark boundaries between the Middle Devonian and the Late Devonian since known Late Devonian beds were found above both bone beds, Olentangy Shale at East Liberty and Huron Shale at Little Hardwick Creek, with observable Middle Devonian limestone underlying both bone beds. I wanted to compare lithological, faunal and conodont biozones to see if the two bone beds correlated to one another. Observations of the lithology both showed that each bone bed contained clastic contents of quartz and phosphate pebbles all contained within a limestone and domomitic matrix. As shown above, using both observational analysis and Sørensen similarity index, the two faunas were identical. The similarities of



the fauna included chondrichthyes, acanthodians and placoderms. East Liberty Bone Bed conodont biozone was determined to be *linguiformis*, 376-376.5 ma. Little Hardwick Creek Bone Bed C conodont biozone was determined to be *triangularis*, 374-376 ma. Chronostratigraphic analysis was ultimately the determining factor used to say that East Liberty Bone and Little Hardwick Creek Bone Bed C do not correlate to one another.

## References

- Armstrong, Howard A., Brasier, Martin D. (2005). Microfossils. *Blackwell Publishing*, Malden, MA.
- Belka, Z., Kaufmann, B., Bultynck, P. (1997). A Conodont-Based Quantitative Biostratigraphy for the Eifelian of the Eastern Anti-Atlas, Morocco. *Geological Society of American Bulletin*, v. 109, pp. 643-651.
- Benton, Michael, Harper, David (1997). Basic Paleontology. *Addison Wesley Longman Limited*, Essex, England.
- Brett, Carlton E., Turner, Alan H., McLaughlin, Patrick I., Over, D. Jeffrey, Storrs, Glenn W., Baird, Gordon C. (2003). Middle-Upper Devonian (Givetian-Famennian) Bone/Conodont Beds from Central Kentucky, USA: Reworking and Event Condensation in the Distal Acadian Foreland Basin. *Cour. Forsch.-Inst. Senckenberg*, vol. 242, pp. 125-139.
- Bultynck, P. (1985). Lower Devonian (Emsian) – Middle Devonian (Eifelian and Lowermost Givetian) Conodont Successions from the Ma' der and the Tafilalt, Southern Morocco. *Courier Forschungsinstitut Senckenberg*, v. 75, pp. 261-286.
- Bultynck, P., Dreesen, R., Groessens, E., Struwe, W., Weddige, K., Werner, R., Ziegler, W. (1988). Field Trip A., in: 1<sup>st</sup> International Senckenberg Conference and 5<sup>th</sup> European Conodont Symposium (ECOS V), Contributions I, Guide to Field Trips. *Courier Forschungsinstitut Senckenberg Senckenberg*, v. 102, pp. 9-155.
- Bultynck, P., Holland, H. (1980). Distribution compare de Conodonts et Goniatices devoniens de plaines du Dra, du Ma' der et du Tafilalt (Maroc). *Aardkundige Mededelingen*, v. 1, pp. 1-73.

- Butts, Charles (1915). Geology and Mineral Resources of Jefferson County, Kentucky. *Kentucky Geological Survey*, v. 3, p. 270.
- Camp, Mark J. (2006). Roadside Geology of Ohio. *Mountain Press*, Missoula, MT.
- Campbell, Guy (1946). New Albany Shale. *Geological Society of America Bulletin*, v. 57, p. 829-908.
- Carroll, Robert L. (1988). Vertebrate Paleontology and Evolution. *W. H. Freeman and Company*, New York, New York.
- Clark, D. L., Ethington, R. L. (1967). Conodonts and Zonation of the Upper Devonian in the Great Basin. *Geological Society of America*, Memoir 103, p. 94.
- Clark, David L., Sweet, Walter C., Bergstrom, Stig M., Klapper, Gilbert, Austin, Ronald L., Rhodes, Frank H. T., Muller, Klaus J., Ziegler, Willi, Lindstrom, Maurits, Miller, James F., Harris, Anita G. (1981). Treatise on Invertebrate Paleontology: Part W: Supplement 2: Conodonta. *The University of Kansas and The Geological Society of America, Inc.*, Boulder, CO.
- Cohee, G. V., Wright, W. B. (1972). Changes in Stratigraphic Nomenclature by the U. S. Geological Survey. *Geological Survey Bulletin*, 1394-A, p. A63-A70.
- Conkin, J. E. (1989). Olentangy Shale and its Correlatives in Eastern United States. *University of Louisville Studies in Paleontology and Stratigraphy*, p. 221-243.
- Conkin, James E., Conkin, Barbara, Steinrock, Larry (1998). Middle Devonian Type Jeffersonville Limestone at The Falls Of Ohio. *University of Louisville in Paleontology and Stratigraphy*, p. 1-64.

- Conkin, J. E. and M. R. Dasari. 1998. Unconformities and Stratigraphic Correlation. *In* Narasimha Rao, K. L., Ed., Progressive probes into Earth Sciences and remote sensing. A Tirupati: Siddhartha Publications. 11–16.
- Donoghue, Phillip C. (1997). Growth and Patterning in the Conodont Skeleton. *The Royal Society*, v. 353, pp. 633-666.
- Duncan, Mags (2006). Various Condrichthyan Microfossil Faunas From the Lower Mississippian (Carboniferous) of Ireland. *Irish Journal of Earth Sciences*, vol. 24, pp. 51-69.
- Feist, R., Klapper, G. (1985). Stratigraphy and Conodonts in Pelagic Sequences Across the Middle-Upper Devonian Boundary, Montagne Noire, France. *Palaeontographica A*, v. 188, pp. 1-8.
- Gabbott, S. E., Aldridge, R. J., Theron, J. N. (1995). A Giant Conodont with Preserved Muscle Tissue From the Upper Ordovician of South Africa. *Nature*, v. 374, pp. 800-803.
- Ginter, Michal (1990). Late Famennian Shark Teeth from the Holy Cross Mountains, Central Poland. *Acta Geologica Polonica*, vol. 40, pp. 69-81.
- Ginter, Michal (2001). Chondrichthyan Biofacies in the Late Famennian of Utah and Nevada. *Journal of Vertebrate Paleontology*, vol. 21, pp. 714-729.
- Ginter, Michal (2002). Chondrichthyan Fauna of the Frasnian-Famennian Boundary Beds in Poland. *Acta Palaeontologica Polonica*, vol. 47, pp. 329-338.

- Ginter, Michal (2002). Taxonomic Notes On “*Phoebodus heslerorum*” and *Symmorium reniforme* (Chondrichthyes, Elasmobranchii). *Acta Palaeontologica Polonica*, vol. 47, pp. 547-555.
- Girard, Catherine, Lecuyer, Christophe (2002). Variations in Ce Anomalies of Conodonts Through the Frasnian/Famennian Boundary of Poland (Kowala-Holy Cross Mountains): Implications for the Redox State of Seawater and Biodiversity. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 181, pp. 299-311.
- Girard, Catherine, Renaud, Sabrina, Serayet, Aurelie (2004). Morphological Variation of *Palmatolepis* Devonian Conodonts: Species Versus Genus. *Comptes Rendus Palevol*, vol. 3, pp. 1-8.
- Gross, W. (1973). Kleinschuppen, Flossenstacheln und Zähne von Fischen aus Europäischen und Nordamerikanischen Bonebeds des Devons. *Palaeontographica A*, vol. 142, pp. 51-155.
- Hansen, Mike (1999). The Geology of Ohio: The Devonian. *Ohio Geological Survey*, p. 1-8.
- Ji, Q., Ziegler, W. (1993). The Lali Section: An Excellent Reference Section for Upper Devonian in South China. *Courier Forschungsinstitut Senckenberg Senckenberg*, v. 157, pp. 1-183.
- Kaufmann, B. (2006). Calibrating the Devonian Time Scale: A Synthesis of U-Pb ID-TIMS Ages and Conodont Stratigraphy. *Earth Science Reviews*, v. 76, pp. 175-190.
- Kaufmann, B., Trapp, E., Mezger, K. (2004). The Numerical Age of the Upper Frasnian (Upper Devonian) Kellwasser Horizons: A New U-Pb Zircon Date from

- Steinbruch Schmidt (Kellerwald, Germany). *Journal of Geology*, v. 112, pp. 495-501.
- Kepferle, Roy C. (2001). Devonian System. *United States Geological Survey*,  
<http://pubs.usgs.gov/pp/p1151h/devonian.html>.
- Klapper, G. (1971). Sequence within the Conodont Genus *Polygnathus* in the New York Lower Middle Devonian. *Geologica et Palaeontologica*, v. 5, pp. 59-72.
- Klapper, Gilbert, Johnson, J. G. (1980). Endemism and Dispersal of Devonian Conodonts. *Journal of Paleontology*, vol. 54, pp. 400-455.
- Klapper, G. (1985). Sequence in Conodont Genus *Ancyrodella* in Lower *asymmetricus* Zone (Earliest Frasnian, Upper Devonian) of the Montagne Noire, France. *Palaeontographica A*, v. 5, pp. 59-72.
- Klapper, G. (1989). The Montagne Noire Frasnian (Upper Devonian) Conodont Succession. In: McMillan, N. J. et al. (eds.). Devonian of the Worlds. *Canadian Society of Petroleum Geologists Memoir*, v. 14, pp. 70-92.
- Klapper, G. (1997). Graphic Correlation of Frasnian (Upper Devonian) Sequences in Montagne Noire, France, and Western Canada. *Geological Society of America Special Papers*, v. 321, pp. 113-129.
- Koussoulakou, Despina S, Margaritis, Lukas H., Kousslakos, Stauros L. (1999). A Curriculum Vitae of Teeth: Evolution, Generation, Regeneration. *International Journal of Biological Sciences*, vol. 5, pp. 226-243.
- Lelievre, H., Derycke, C. (1998). Microremains of Vertebrate near the Devonian Carboniferous Boundary of Southern China (Hunan Province) and Their

- Biostratigraphical Significance. *Revue de Micropaleontologic*, vol. 41, pp. 297-320.
- Long, John A. (1990). Late Devonian Chondrichthyans and Other Microvertebrate Remains from Northern Thailand. *Journal of Vertebrate Paleontology*, vol. 10, pp. 59-71.
- Maisey, John G. (1989). Visceral Skeleton and Musculature of a Late Devonian Shark. *Journal of Vertebrate Paleontology*, vol. 9, pp. 174-190.
- Maisey, John G. (1996). Discovering Fossil Fishes. *Westview Press*, Boulder, CO.
- Mann, Keith O., Wambsgans, Cynthia, Everett, Randy (2007). The Stratigraphy of the East Liberty Quarry (Logan County, Ohio) in the Bellefontaine Outlier. *Geological Society of America Abstracts with Programs*, v. 39., p. 72.
- Murphy, M. A. (2000). Conodonts First Occurrences in Nevada. In: Weddige, K. [ed.]. Devonian Correlation Table, *Senckenbergiana lethaea*, v. 80, p. 695.
- Nichols, Gary (1999). Sedimentology and Stratigraphy. *Blackwell Science*, Malden, MA.
- Over, D. Jeffrey (2007). Conodont Biostratigraphy of the Chattanooga Shale, Middle and Upper Devonian, Southern Appalachian Basin, Eastern United States. *Journal of Paleontology*, vol. 8, pp. 1194-1217.
- Over, D. Jeffrey, Rhodes, Meredith K. (2000). Conodonts from the Upper Olentangy Shale (Upper Devonian, Central Ohio) and Stratigraphy Across the Frasnian-Famennian Boundary. *Journal of Paleontology*, vol. 74, pp. 101-112.
- Prothero, Donald R. (2004). Bringing Fossils to Life: An Introduction to Paleobiology. *The McGraw-Hill Companies, Inc.*, p. 1-503.

- Richards, B. C., Ross, G. M., Utting, J. (2002). U-Pb Geochronology, Lithology and Biostratigraphy of Tuff in the Upper Famennian to Tournaisian Exshaw Formation: Evidence for a Mid-Paleozoic Magmatic Arc on the Northwestern Margin of North America. *Canadian Society of Petroleum Geologists Memoir*, v. 19, pp. 158-207.
- Roden, M. K., Parrish, R. R., Miller, D. S. (1990). The Absolute Age of the Eifelian Tioga Ash Bed, Pennsylvania. *Journal of Geology*, v. 98, pp. 282-285.
- Roen, J. B., Kepferle, R. C. (1993). Petroleum Geology of the Devonian and Mississippian Black Shale of Eastern North America. *United States Geological Survey Bulletin*, p. B1-B57.
- Romer, Alfred Sherwood, Williams, George C. (1976). The Early Evolution of Fishes. *The Quarterly Review of Biology*, vol. 51, pp. 202-240.
- Rotondo, K. A., Over, D. J. (2000). Biostratigraphic Age of the Belpre Ash (Frasnian), Chattanooga and Rhinestreet Shales in the Appalachian Basin. *Geological Society of America Abstracts and Programs*, v. 32, p. A70.
- Savage, Norman M. (1995). Middle Devonian Conodonts from the Wadleigh Limestone, Southeastern Alaska. *Journal of Paleontology*, vol. 69, pp. 540-555.
- Savage, Thomas Edmund (1931). The Devonian Fauna of Kentucky. P. 217-247. In W. R. Jillson (1931), *The Paleontology of Kentucky*. Kentucky Geological Survey, v. 36, series 6.
- Sharks-Teeth. 2010. <http://www.sharks.org.za/teeth.html>.
- Shaver, R. H., Ault, C.H., Burger, A. M. (1986). Compendium of Rock-Unit Stratigraphy in Indiana. *Indiana Geological Survey Bulletin*, v. 59, p. 203.



- Sparling, Dale R. (1983). Conodont Biostratigraphy and Biofacies of Lower Middle Devonian Limestones, North-Central Ohio. *Journal of Paleontology*, vol. 57, pp. 825-864.
- Sparling, Dale R. (1995). Conodonts from the Middle Devonian Plum Brook Shale of North-Central Ohio. *Journal of Paleontology*, vol. 69, pp. 1123-1139.
- Sparling, Dale R. (1999). Conodonts from the Prout Dolomite of North-Central Ohio and Givetian (Upper Middle Devonian) Correlation Problems. *Journal of Paleontology*, vol. 73, pp. 892-907.
- Stauffer, C. R., Hubbard, G. D., Bownocker, J. A. (1911). Geology of the Columbus Quadrangle. *Geological Survey of Ohio Bulletin*, v. 14, p. 1-133.
- Stensio, E. (1961). Permian Vertebrates (From East Greenland). pp. 231-247 in G. O. Raasch, ed. *Geology of the Arctic, University of Toronto*, Toronto.
- Stensio, E. (1962). Origine et nature des ecailles placoides et des dents. In J. P. Lehman, ed. *Problemes actuels de paleontologie (evolution des vertebres). Colloques Internationaux du Centre National de la Recherche Scientifique*, vol. 104, pp. 297-320.
- Stewart, Grace Anne, Sweet, Walter C. (1956). Conodonts from the Middle Devonian Bone Beds of Central and West-Central Ohio. *Journal of Paleontology*, vol. 30, pp. 261-273.
- Streel, M. (2000). The Late Famennian and Early Frasnian Datings Given by Tucker and Others are Poorly Constrained. *Subcommission on Devonian Stratigraphy, Newsletter*, v. 17, p. 59.

Symmmoriida. *Academic Dictionaries and Encyclopedias*,

<http://de.academic.ru/dic.nsf/dewiki/1352815>.

Trapp, E., Kaufmann, B., Mezger, K., Korn, D., Weyer, D. (2004). Numerical Calibration of the Devonian–Carboniferous Boundary: Two New U-Pb Isotope Dilution-Thermal Ionization Mass Spectrometry Single-Zircon Ages from hasselbachtal (Sauerland, Germany). *Geology*, v. 32, pp. 857-860.

Tucker, R. D., Bradley, D. C., Ver Straeten, C. A., Harris, A. G., Ebert, J. R., McCutcheon, S. R. (1998). New U-Pb Zircon Ages and the Duration and Division of Devonian Time. *Earth and Planetary Science Letters*, v. 158, pp. 175-186.

Turner, Susan (1982). Middle Palaeozoic Elasmobranch Remains from Australia. *The Journal of Vertebrate Paleontology*, vol. 2, pp. 117-131.

Ver Straeten, C. A. (2001). Emsian-Eifelian (Lower-Middle Devonian) of Virginia-West Virginia, and a Basinwide Synthesis and Sequence Stratigraphy. *Geological Society of America America Abstracts and Programs*, v. 33, p. A61.

Weddige, K. (1977). Die Conodonten der Eifel-Stufe im Typusgebiet und in benachbarten Faziesgebieten. *Senckenbergiana lethaea*, v. 58, pp. 271-419.

Weddige, K. (1996). Devon-Korrelationstabelle. *Senckenberiana lethaea*, v. 76, pp. 267-286.

Wells, John (1944). Fish Remains From the Middle Devonian Bone Beds of the Cincinnati Arch Region. *Paleontographica Americana*, v. 16, p. 105-113.

Williams, M. E. (1979). The “Cladodont Level” Sharks of the Pennsylvanian Black Shales of North America. Unpublished Ph. D. Dissertation, University of Kansas, p. 203.

- Whitenack, Lisa B., Elliot, Dana R., Brandenburg, J. P. (2002). A Case Study in Paleoeology from the Mississippian of Missouri, with a Focus on Chondrichthyan Teeth. *Transactions of the Missouri Academy of Science*, vol. 36, pp. 7-10.
- Yolkin, E. A., Weddige, K., Izokh, N. G., Erina, M. V. (1994). New Emsian Conodont Zonation (Lower Devonian). *Courier Forschungsinstitut Senckenberg*, v. 168, pp. 139-157.
- Zangerl, Rainer (1981). Handbook of Paleoiichthyology: Chondrichthyes I (Paleozoic Elasmobranchii). *Gustav Fischer Verlag*, Stuttgart, NY.

## **Appendix I: Superclass Agnathans**

Agnathans represent a complex array of “jawless” vertebrates. Today, there are only two living examples, hagfish, the Myxiniiformes, and lampreys, the Petromyzontiformes. Agnathans evolved during the Late Cambrian. Ostracoderms, or “shell-skinned fishes”, were the earliest agnathan group. They represent a several distinct taxonomic groups, and thus form a paraphyletic clade. Ordovician ostracoderms had a head shield made up of both large and small plates. Their remains can be found in the Silurian Harding Sandstone, in Colorado. The Harding Sandstone was thought to have formed in a near shore, high energy shallow sea; therefore the early ostracoderms inhabited near shore, high energy shallow waters (Carroll, 1988; Maisey, 1996).

Heterostracans appeared during the Silurian Period and existed throughout the Devonian Period. The heterostracans differ from the early Ordovician ostracoderms in that they have gills that open to the external environment, one opening on each side of their body. Heterostracans reached a maximum length of only several centimeters. Paired fins and dorsal fins were both absent. They had a reversed tail and a flattened body, possibly enabling them to live near the bottom of the water, thus avoiding the high energy waters above where their anatomy could not support them. Heterostracans evolved rapidly and began colonizing new habitats, including freshwater environments (Maisey, 1996).

Osteostracans were a very diverse group of agnathans. They first appeared during the Late Silurian. Morphologically diverse, both primitive and advanced osteostracans were both found together during the Late Silurian, indicating an earlier origination time than the first appearance in the fossil record. Osteostracans are only found in northern

areas, including North America, Greenland and northern Europe. The more advanced forms inhabited lagoons in the Late Silurian. During the Devonian osteostracans began diversifying both taxonomically and geographically, with differential success. Early osteostracans are found in marine sediments, including marginal marine and lagoonal deposits. Later osteostracans are found in freshwater deposits, including streams and lakes. *Hemicyclapis* was a very successful genus that persisted throughout the Devonian inhabiting freshwater environments (Carroll, 1988; Maisey, 1996).

An important feature shared by osteostracans and gnathosomes is the presence of a pair of front fins, a heavy carapace and a well ossified endochondral braincase. The pair of front fins, along with a small dorsal fin, allowed osteostracans to swim more efficiently than heterostracans. The mouth and gill openings were located beneath the head, a characteristic of modern rays, thus suggesting they lived a benthic existence, feeding on organic material and invertebrates (Carroll, 1988; Maisey, 1996).

Galeaspids, another type of agnathan, share a close resemblance to osteostracans. The fossil record indicates first appearances in the Silurian with the last appearance in the Devonian. Galeaspids occupied southern Gondwana waters and are thought to be the southern osteostracans. They had no paired fins and lacked cell spaces in bone tissue, a diagnostic characteristic of differences between most osteostracans and gnathosomes (Maisey, 1996).

Anaspids were the most streamlined of all agnathans, indicating that they were much more active swimmers than the rest of the osteostracans. Anaspids are puzzling because they evolved in the Early Silurian and went extinct in the Late Devonian, but they lack a fossil record during the middle of that interval. Furthermore, preservation of

anaspids is usually quite poor. Without more evidence, it is difficult to systematically place anaspids as either related to lampreys or related to jawed bony fish. When found, anaspid remains are associated with freshwater deposits. Annular-like cartilage has been observed around their mouth in some fossil specimens. They had an overall fusiform body shape. The gill openings were located behind each eye and progressively, over time became more ventrally located. The annular like cartilage and gill openings are both common characteristics shared with the lampreys. Characteristics shared with jawed bony fishes include paired front fins, dermal bones around the eyes and a large dermal plate beneath the mouth (Carroll, 1988; Maisey, 1996).

Thelodonts had a worldwide distribution, inhabiting seas across the globe. The first appearance of thelodonts was during the Late Ordovician with their last appearance in the Late Devonian. Their worldwide distribution lends support to the idea that they were efficient swimmers. Some thelodonts had paired pectoral fins on each side of their body, as well as a dorsal and anal fin. They had abundant amounts of shark-like scales. Thelodonts entire body was covered by rhomboidal, nonimbricating scales, which had no bone cells in the basal region. It is currently thought thelodonts may have given rise to the jawed-fishes. Supporting evidence includes pharyngeal scales, as well as a stomach, a highly specialized organ with digestive enzymes. Early thelodont remains can be found in marine sediments and later thelodonts eventually invaded freshwaters (Carroll, 1988; Maisey, 1996).

## **Appendix II: Class Conodonta**

Conodonts first appeared in the fossil record in during the Late Cambrian. These primitive jawless vertebrates evolved rapidly until their demise in the Late Triassic. Whole specimens are not commonly found in the fossil record, with exception to the Granton Shrimp Beds near Edinburgh (Briggs et al., 1983). The overall anatomies of conodonts are based on these well preserved, whole specimens. However, the fossil record has bountiful examples of their calcium phosphate oral and pharyngeal elements, which comprise their feeding apparatus (Clark, 1981; Armstrong, et. al., 2005).

Conodonts ranged in size from microscopic to a length of about 40 mm, with an eel-like body shape. The trunk region was composed of a notochord, chevron shaped muscle blocks and caudal fin rays. The head region had sclerotic cartilages surrounding their eyes, which are located behind the sclerotic cartilage (Fig. 18) (Clark, 1981; Gabbott et al., 1995; Armstrong, et. al., 2005).

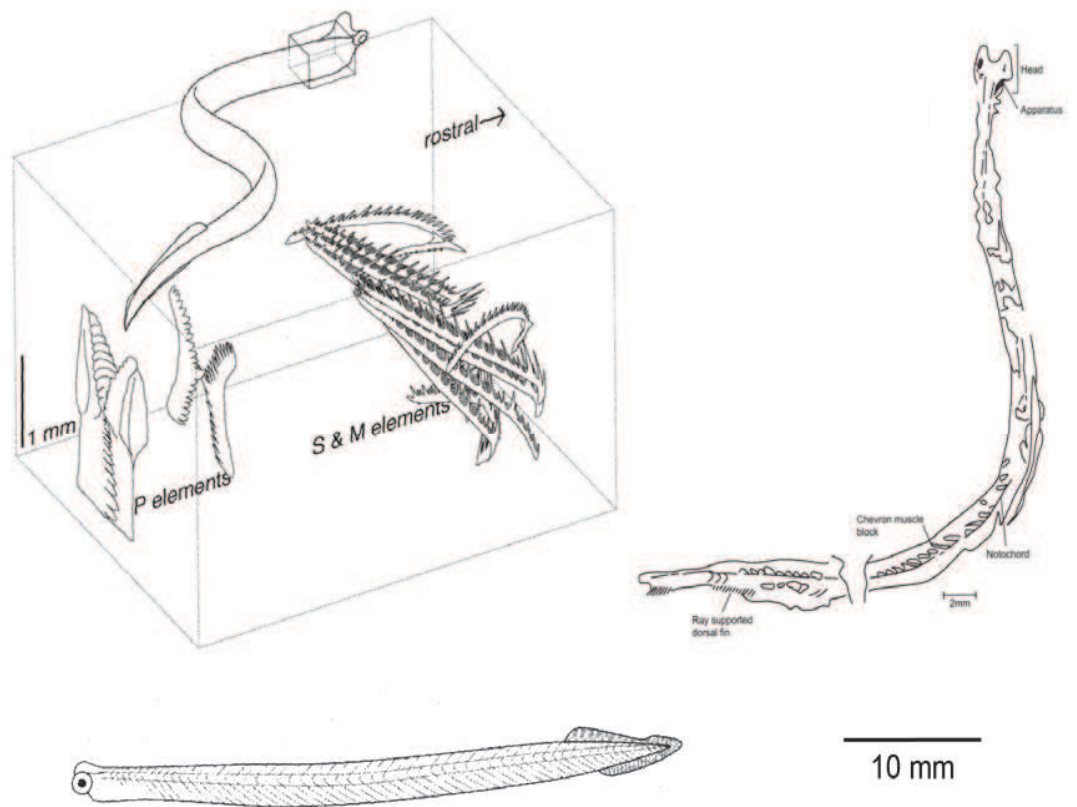


Figure 18. General anatomy of a conodont (Armstrong et al., 2005; Benton, 2005).



Pre-Mississippian Period conodont elements are composed of two parts, the basal body and the crown. The basal body was located in the basal cavity of the crown. The crown is composed of an internal opaque tissue, which gives the elements their color when observed (Armstrong et al., 2005). Additionally, the crown is composed of hyaline and lamella tissue with growth lines. Growth lines form from the addition of layers of crown enamel, making the inner lamella the oldest (Fig. 19) (Clark et al., 1981; Donoghue, 1997).

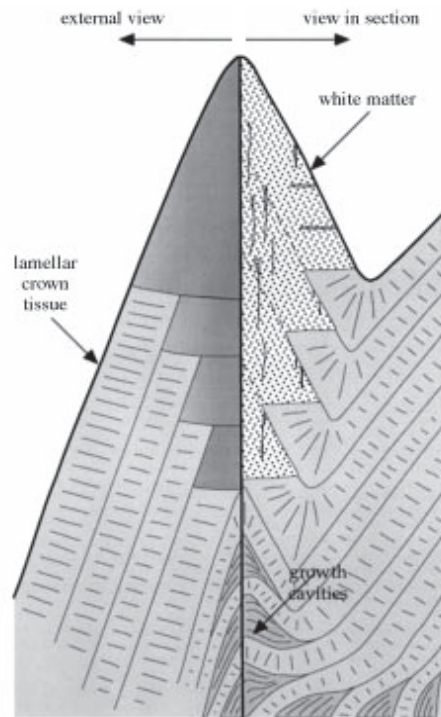


Figure 19. Growth lines of a conodont element (Donoghue, 1997).

Non-coniform taxa and coniform apparatuses are composed of one of two morphological domains. Non-coniform taxa apparatuses have a rostral domain with paired *S* elements, a pair of dorso-lateral *M* elements, and a caudal domain consisting of up to four pairs of *P* elements. The paired *S* elements generally consist of *Sa*, *Sb*, *Sc*, and *Sd* components. *Pa*, *Pb*, *Pc* and *Pd* elements represent the dorso-lateral *P* elements (Fig. 20).

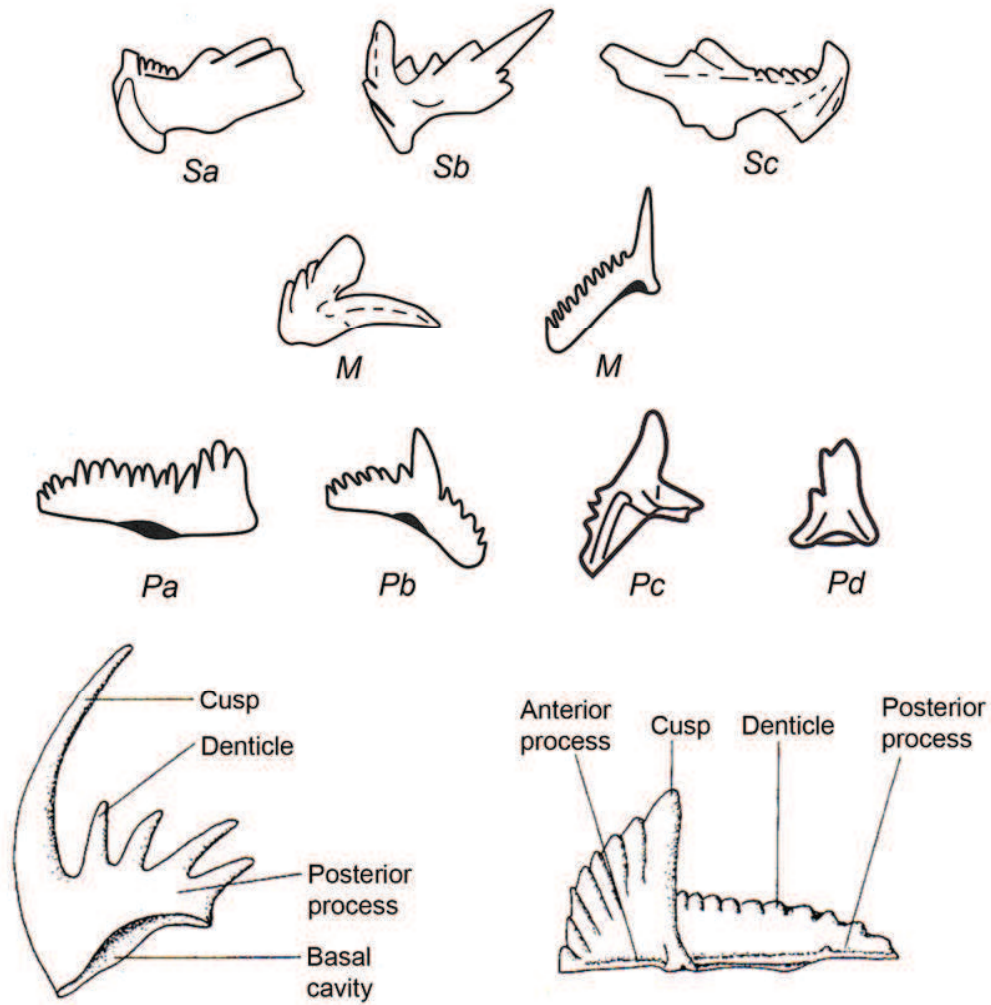


Figure 20. Diagram showing S, P and M processes found in the apparatuses of conodonts (Prothero, 2004; Armstrong, 2005).

Coniform apparatuses are composed of a rostral domain, composed of  $q$  elements (*costate*), and a caudal domain, composed of  $p$  elements (*acostate*). The  $q$  elements consist of  $qa$ ,  $qg$  and  $qt$  components. The  $p$  elements are represented by  $pf$  and  $pt$  components (Fig. 21) (Clark et al., 1981; Armstrong, et. al., 2005).

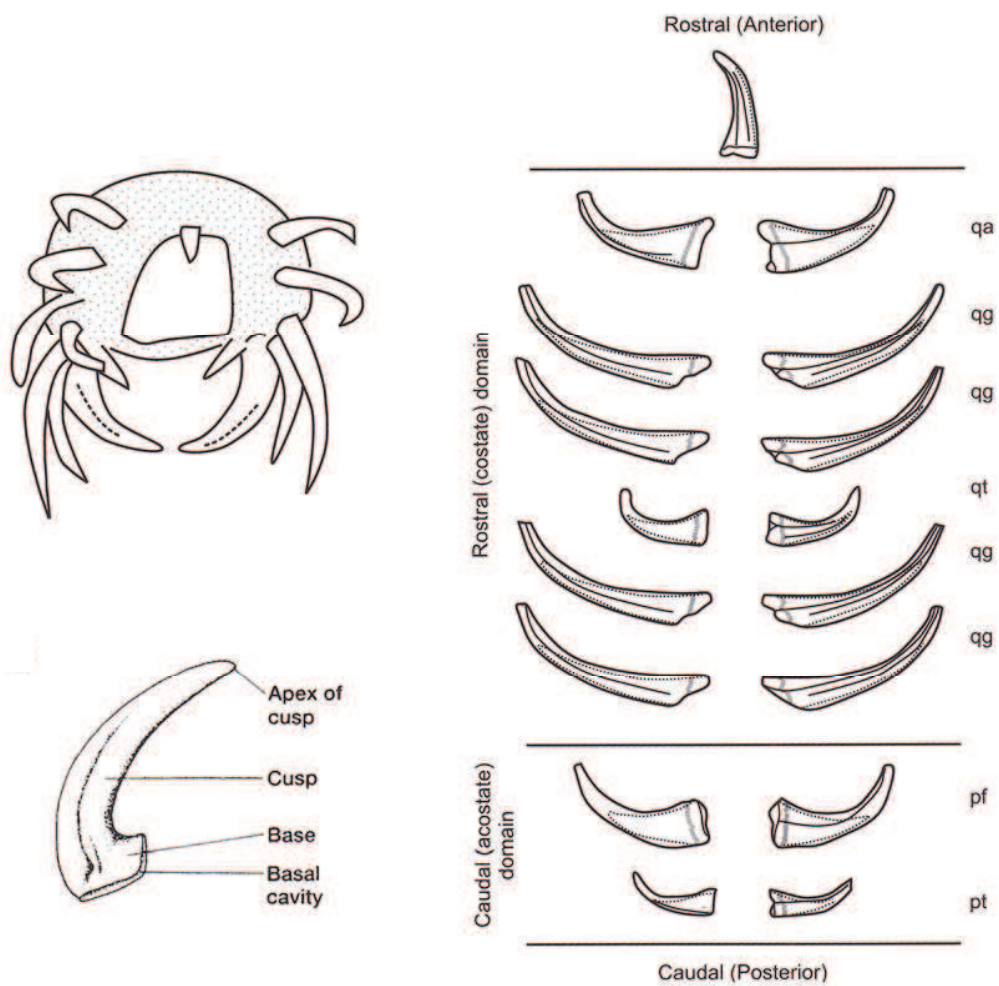


Figure 21. Q and P conodont elements (Prothero, 2004; Armstrong, 2005).

Elements are classified by the position of their cusps. Elements with a dorsal process are classified by the number of primary processes they possess. *Segminate* elements have a dorsal process that is composed of a single or multiple rows of nodes or ridges. *Carminate* elements have a straight aboral margin and are composed of dorsal and ventral processes. If an element has three primary processes, one of them being a dorsal process, then they are classified as *pastinate* elements. If an element has four primary processes, one of them being a dorsal process, then they are classified as *stellate* elements (Table 1) (Clark et al., 1981; Armstrong, et. al., 2005).

<b>Types of Processes</b>	<b>Characteristics</b>
Segminate	Dorsal process with single or multiple rows of nodes or ridges
Carminate	Possess a straight aboral margin, dorsal and ventral processes
Pastinate	Have three primary processes
Stellate	Have four primary processes

Table 1. Types of processes for conodont elements with dorsal processes.



Elements without a dorsal process are termed dolabrate, alate, bipennate, digyrate, extensiform digyrate, breviform digyrate, tertiopedate, quadriramate or multiramate elements. Dolabrate elements have caudal process and are T shaped. Alate elements have a caudal process flanked by lateral processes on each side making it bilaterally symmetrical. Bipennate elements have a caudal process and a shorter rostral process that curves towards the caudal process. Digyrate elements have caudal processes that are flanked on each side by lateral processes. The caudal processes are less developed in digyrate elements than those found in alate elements. Digyrate elements are asymmetrical with respect to the lateral processes, since they twist and turn in opposing directions. Extensiform digyrate elements have their lateral processes curving towards their distal ends of the element. These lateral processes grow much longer as compared to the lateral processes found in digyrate elements. Breviform digyrate elements have short lateral processes that bend from the base of the cusp. Tertiapedate elements have a caudal process and lateral processes that are arranged asymmetrical around the cusp. Quadriramate elements have four processes, rostral, caudal and two lateral processes. Multiramate elements are any elements with more than four processes, although none have been observed (Table 2) (Fig. 22) (Clark et al., 1981; Armstrong, et. al., 2005).

<b>Types of Processes</b>	<b>Characteristics</b>
Dolabrate	Caudal processes, T shaped
Alate	Caudal processes with bilaterally symmetrical lateral processes
Bipennate	Caudal processes, short rostral processes that is inclined towards the caudal process
Digyrate	Caudal processes that are flanked by asymmetrical lateral processes
Extensiform Digyrate	Lateral processes are inclined to their distal ends
Breviform Digyrate	Short lateral processes that bend at the base
Tertiapedate	Caudal processes and asymmetrical lateral processes around the cusp
Quadriramate	Have four processes: rostral, caudal and two lateral processes
Multiramate	Any elements with more than four processes

Table 2. Types of processes for conodont elements without a dorsal process.

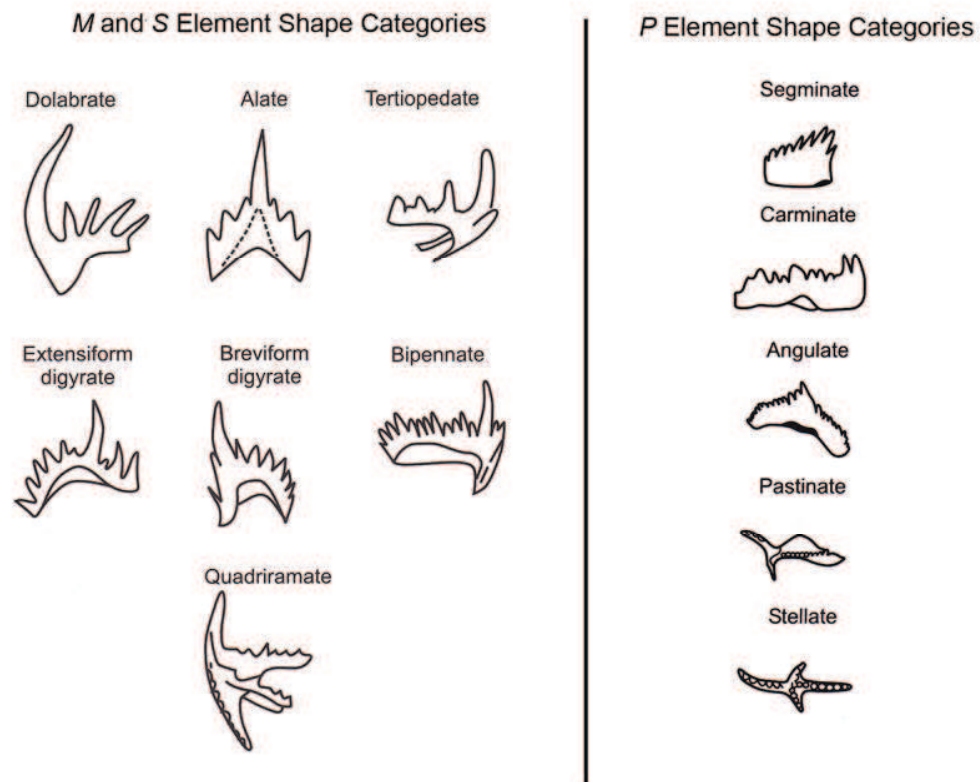


Figure 22. Shape categories for M, S and P conodont elements (Armstrong et al., 2005).

There are two proposed theories as to the function of the feeding apparatus. First, the feeding apparatus was used for microphagous suspension feeding. This theory proposes that the S and M elements were used as support for a soft ciliated sieve structure that was used to filter foodstuffs. The p elements were responsible crushing the foodstuffs. The second theory proposes a microphagous suspension feeding, where the S and M elements were actively grasping foodstuffs from the water while the p elements sliced and crushed foodstuffs (Clark, 1981; Girard et al., 2004; Armstrong et. al., 2005).

Conodonts have been used extensively to develop biostratigraphic zones throughout the Devonian Period (Stewart et al., 1956; Klapper, 1980; Sparling, 1983; Savage, 1995; Sparling, 1995; Sparling, 1999; Over et al., 2000; Girard et al., 2002; Girard et al., 2004; Armstrong, 2005; Over, 2007). These abundant, yet enigmatic marine vertebrates are found mostly in near shore in calciclastic facies (Benton, et. al., 1997). The Givetian Stage of the Middle Devonian is subdivided into seven different biozones: *norrissi*, *timorensis*, *rhenanus*, *ansatus*, *hermanni*, *latifossatus* and *disparilis*. The Frasnian Stage of the Upper Devonian can be divided into the *norrissi*, *falsiovalis*, *transitans*, *puntata*, *hassi*, *jamiae*, *rhenana*, and *linguiformis* conodont zones. The Famennian Stage can be divided into the *triangularis*, *crepida*, *rhomboidea*, *marginifera*, *trachytera*, *postera*, *expansa* and *praesulcata* conodont zones (Fig. 23) (Sparling, 1956; Klapper, 1980; Sparling, 1983; Savage, 1995; Sparling, 1995; Over et al., 2000; Girard et al., 2002, Brett et al., 2003, Girard et al., 2004; Armstrong, et. al., 2005; Kaufmann, 2006; Over, 2007).



### **Appendix III: Intraphylum Gnathostomata**

Gnathosomes include all of the jawed fishes. The evolutionary development of jaws increased predation in the early oceans. Jawed-fish were able to prey upon each other. The development of jaws also forced fish to adapt to predation, thus causing them to move more effectively and be to become efficient swimmers. The fish that became more adapted to swimming were not only able to escape predation more easily but they also became the apex predators of the seas (Maisey, 1996).

Fossil evidence points to a gnathosome explosion during the Early Devonian. This explosion resulted in a highly diverse assemblage of diversity on all taxonomic levels. This high diversity, especially at higher taxonomic levels and body-plans, was never again achieved after the Late Devonian. (Maisey, 1996).

#### **III.I: Class Acanthodii**

Acanthodians first appear in the fossil record during the Late Silurian and disappeared from the fossil record during the Permian. The group spanned 160 million years with very few genera, in comparison to the length of their existence. These fusiform, spiny fish were very small, one to a several inches in length. They possessed a hyostolic jaw. Acanthodians had a heterocercal tail much like that of sharks. Acanthodians had median and paired fins which were supported by spines. Anal fin and dorsal fins were also supported by spines, possibly for defensive purposes (Carroll, 1988). Within the Order Acanthodii, advanced forms with fewer intermediate spines are known (Romer et al., 1976; Maisey, 1996).

Acanthodians are believed to be closely related to the ray finned fishes. Fritsch (1895) was the first to point to the ancestral relationship of acanthodians with the ray finned fishes, but his evidence, in the form of a well preserved specimen, was not discovered until the late 1980s. Fritsch documented that the gill lamellae on each gill are separate, the same feature as in ray finned fishes. Fritsch also observed that acanthodians had three pairs of otoliths, a feature found in modern ray finned fish. Another compelling characteristic shared between acanthodians and ray finned fishes are that their bodies are completely covered by ganoid scales (Romer, et al., 1976; Maisey, 1996). These scales were not overlapping and they resembled elasmobranchs dermal denticles. The absence of a pulp cavity distinguished them from earlier chondrichthyes. Scales were composed of a dentine-like superficial portion and a deep bony base. Teeth were not found in all genera. General that did have teeth were classified into three types: tooth whorls, isolated elements and teeth fused to the jaws (Carroll, 1988).

### **III.II: Class Placodermi**

The placoderms were a very diverse group of jawed-fishes that existed throughout the Devonian. Members of this group were among the top predators of Devonian seas. Their jaws were modified forming tooth-like protrusions, made from bony plates, incorporated into their jaws. Their upper and lower jaws could contract, with great force, joining together in perfect alignment for sharpening their modified jawed parts, as well as tearing apart captured prey. Placoderms had a jointed neck which allowed them to gape their mouth much larger than otherwise would be the case. Placoderms were covered in armor plates on their head and chest region (Fig. 24). There were two major groups of

placoderms: the antiarchs (Fig. 25) and arthrodiros (Fig. 26) (Romer et al., 1976; Maisey, 1996).



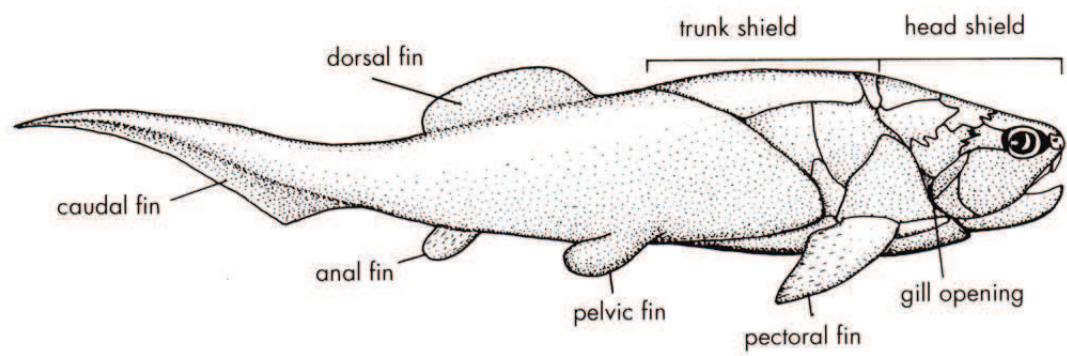


Figure 24. External anatomy of a placoderm (Long, 1996).

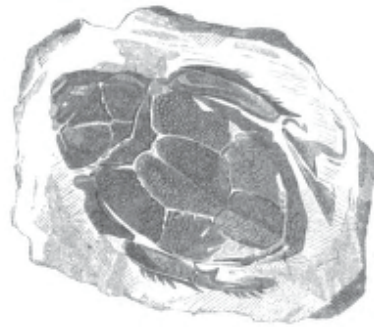


Figure 25. Antiarch specimen found in Dura Den (Anderson, 1859).



Figure 26. An example of an arthrodire, *Dunkleosteus terrelli*. (Arreola, 2005).

Antiarchs first appeared in the Silurian but did not diversify until the Early to Middle Devonian. Changes in sea level and the ability to outcompete the less advanced agnathans probably allowed them to dominate shallow benthic environments. Antiarchs have been found on every continent, in both marine and freshwater deposits, probably originating in the later environment (Romer et al., 1976; Carroll, 1988; Maisey, 1996).

Antiarchs had a body encased in a flat bony box. They had pair of appendages projecting laterally that resembled crab legs. They also had eyes that protruded, somewhat similar to insect eyes (Maisey, 1996). Antiarchs had a very long trunk shield and ossification behind their pectoral fin and posterior lateral and posterior medioventral plates. Nearly all genera are dorsoventrally flattened. Migration of the orbits in the head region to a more dorsal position differs drastically from arthrodires. The internal skeleton is not ossified. In most genera, the head shields is smaller than the trunk shield (Carroll, 1988).

The most advanced antiarchs are the Sinolepids and Bothriolepids. Sinolepids can only be found in China and Australia. Bothriolepids were widespread and found in both marine and freshwater deposits. *Bothriolepis* shared the same environments as lung fishes. It is thought that *Bothriolepis* was able to breathe out of the water and crawl, thus providing an explanation for their peculiar look (Maisey, 1996). Denison (1941), dissected several well preserved fossil specimens and found evidence for two sacs that could be interpreted as lungs, found on either side of the pharynx. Denison suggested that *Bothriolepis* was a facultative fish, breathing air and absorbing oxygen from the water. While this is speculative at best, no other explanation has been given to the sac like structures (Denison, 1941).

The other major placoderm group is the arthrodires which compose two-thirds of all placoderms. The arthrodires had two pairs of upper jaw tooth plates, instead of one found in all other placoderm groups. Most arthrodires were bottom dwellers, but some were free swimming fish which had modified armor allowing more elusive swimming capabilities. Most were small, less than a meter, but some, such as *Dunkleosteus*, reached giant proportions (Maisey, 1996).

Dinichthyans were well armored bony fishes, with a distinctive ball and socket joint between the head and thoracic regions. This ball and socket allowed the upper jaw to move freely while the bottom jaw was at a fixed position. Mastication proceeded by moving the upper jaw up and down, which allowed chewing, but also to increase the gape of their mouth. The post-cephalic region of dinichthyans is best known from the genus *Coccosteus*. *Coccosteus*, a relatively smaller member of the group had a heterocercal caudal fin, dorsal fin, anal fin, paired appendages at the point of the pelvic girdle, pelvic fins extending from the pelvic girdle and pectoral fins behind the shoulder girdle with an anterior spine (Romer et al., 1976; Maisey, 1996).

One of the more advanced forms of dinichthyans was the robust *Dunkleosteus*. *Dunkleosteus* reached up to six meters in length with armor covering more than one meter of the body. It is widely thought that *Dunkleosteus* was the apex predator of the Late Devonian sea. Numerous specimens of *Dunkleosteus terrelli*, and many other dinichthyans, have been found in northeastern Ohio within the Cleveland Shale Member of the Ohio Shale. Bones of *Dunkleosteus* often show puncture wounds that are spaced accordingly to fit the spacing of *Dunkleosteus* tooth plates, thus these puncture wounds

have been interpreted as mating behaviors much like those found in *Carcharodon carcharias* (Romer et al., 1976; Maisey, 1996).

The most primitive group within the arthrodires was the arctolepids. Hollow cones of bone were found in place of shoulder spines. These hollow bones were very stiff and pointed towards the back of their body. The function is not entirely known but it is thought that they used them as a holdfast (Carroll, 1988). The hollow bones may have provided stability along the bottom sediments of lakes or streams which they occupied. They flourished during the Early Devonian until their during the extinction event in the Early Devonian (Romer et al., 1976; Maisey, 1996).

### **III.III: Class Chondrichthyes**

Modern Chondrichthyes are classified into two groups: elasmobranchs (Fig. 27) and holocephalians (Fig. 28).

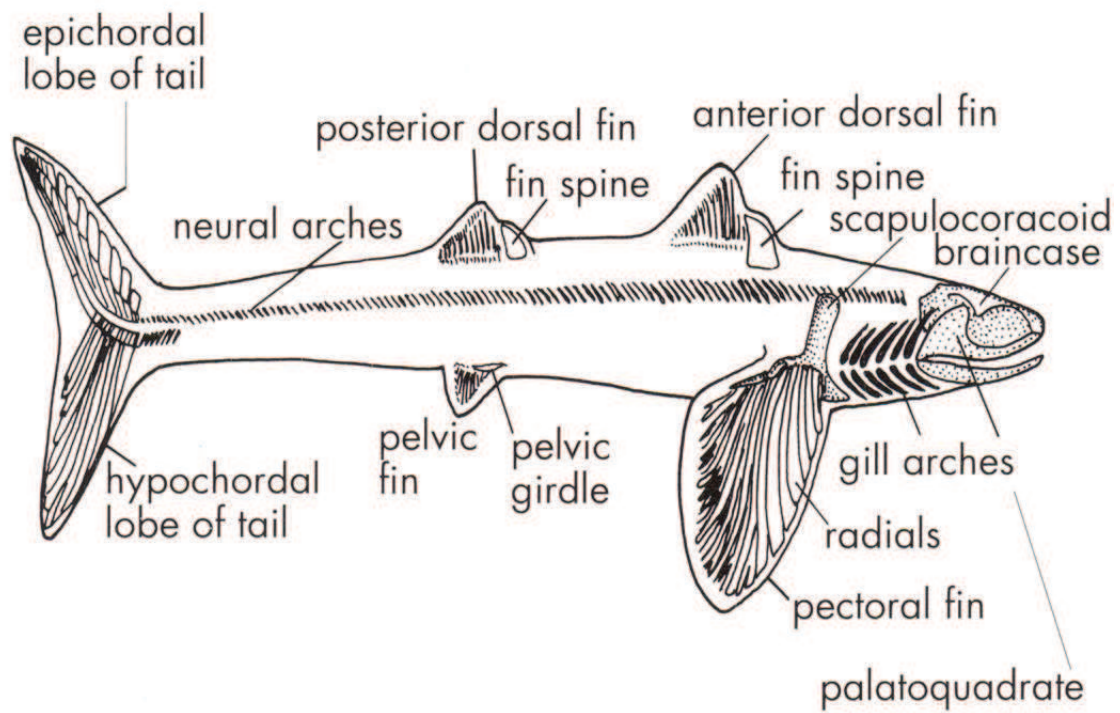


Figure 27. Elasmobranch external anatomy (Benton, 2005).

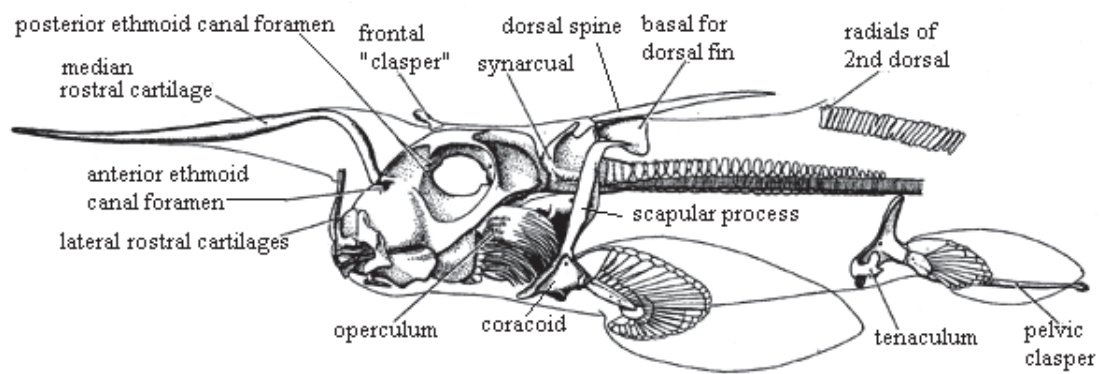


Figure 28. Holocephalian anatomy (Patterson, 1965).



The elasmobranchs include sharks, skates and rays. The holocephalians are composed of the chimaeroids such as the rabbitfish. Holocephalians differ in several morphological aspects from that of the elasmobranchs, including; a holostylic jaw suspension, where the palatoquadrate is fused to the neurocranium, an opercular membrane covering the gills, permanently growing teeth, elongated bodies, slender tail and clasper organs on top of their head. Elasmobranchs and chimaeroids share the characteristics of revolving tooth assembly (Fig. 29), heterocercal tails, nonspine bearing synarcuals and claspers (Zangerl, 1981; Whitenack et al., 2002).



Figure 29. Photograph from a modern mako shark clearly showing the revolving dentition characteristic of sharks (<http://www.sharks.org.za/teeth.html>).

Chondrichthyans possess one of three jaw suspension morphologies: holostylic, amphistylic or hyostylic. Holostylic or autostylic suspension is characterized by the close association between the palatoquadrate and the braincase resulting in fusion. This condition is found in most holocephalians. Amphistylic suspension is characterized by the lower jaw supported by two points, one directly with the postorbital process of the braincase, and the other support in contact with the hyomandibular arch. Cladoselachians had an amphistylic support. Hyostylic jaw suspension occurs when there is a separation between the palatoquadrate and the braincase. The hyomandibular connects the palatoquadrate to the braincase. This condition is found among more advanced elasmobranchs (Fig. 30) (Carroll, 1988).

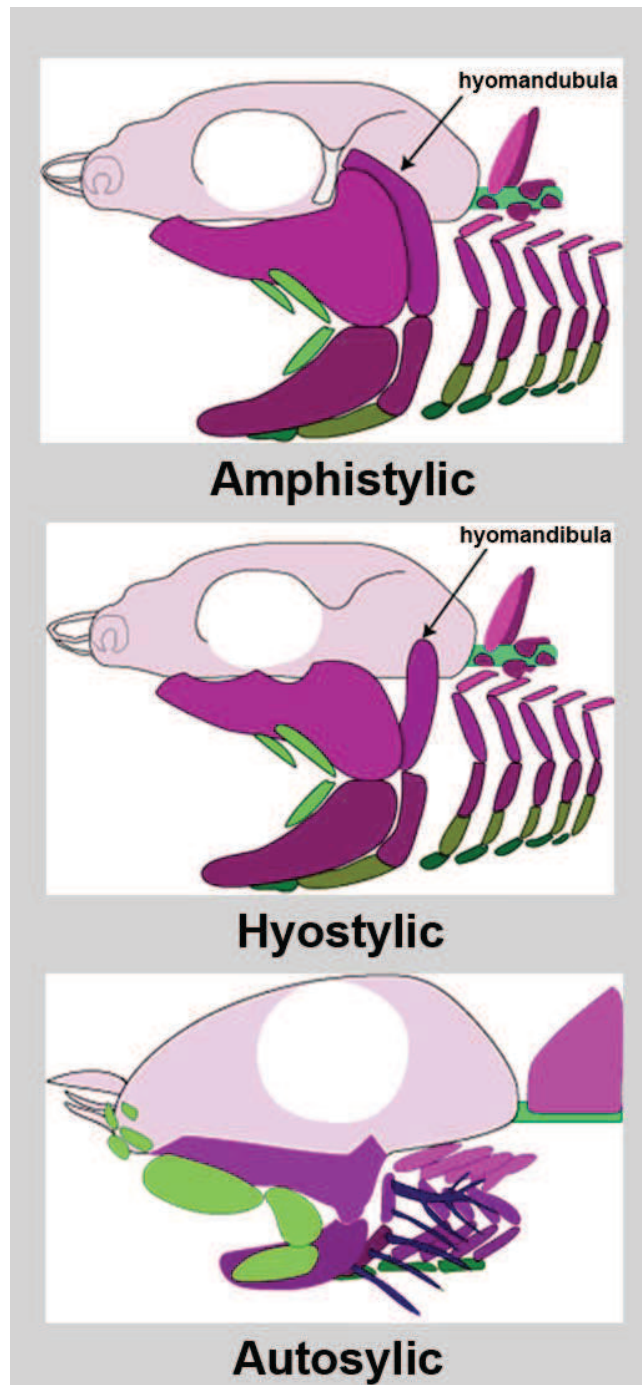


Figure 30. Different jaw suspensions found in chondrichthyans (C. Ciamapaglio).

Most Paleozoic elasmobranchs resemble that of the living dogfish. They had a streamlined, fusiform body and terminal mouth. They had no anal fins. Their heterocercal tail is derived from the notochord axis being pointed directly dorsally. They possessed triangular, broad paired fins. Their braincase was broad and low like with three main regions: ethmoid, orbital region and the otico-occipital region. Extending along most of the braincase was the cleaver shaped palatoquadrate, with an anterior narrow handle and a posterior blade. The anterior handle supports the teeth. The posterior blade allows for musculature support in the medial axis (Carroll, 1988).

Chondrichthyans from the Middle Devonian through the Quaternary have provided a rich fossil record, consisting primarily of complete and associated dentitions, isolated teeth, spines, and denticles, although whole animals are found with some frequency (Brett et al., 2003). Chondrichthyan teeth are comprised of an open pulp cavity beginning at the base (root) and extending to the crown, covered by a layer of orthodentine, followed by a layer of virodentine (enameloid) covering the orthodentine. Teeth form within an invagination of the epithelium within the dental lamina. The dental lamina runs across the lingual side of the jaws. The dental lamina and newly forming teeth are protected from the mouth cavity by a flap of mucosa. Chondrichthyans have parallel rows of teeth. Development starts with the tooth anlagen positioned so that the crowns are in a position of use. Growth of the teeth continues as the teeth rotate to the functional position, where growth ultimately stops. Revolving dentition allows proportional growth of new teeth to match the growth of the animal. (Fig. 31) (Fig. 32) (Zangerl, 1981; Carroll, 1988).

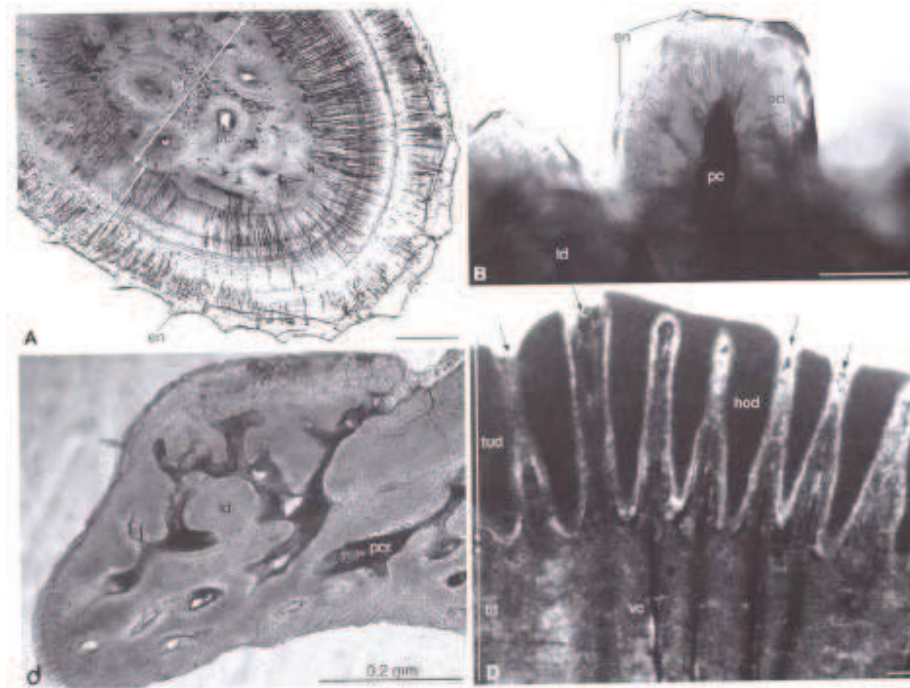


Figure 31. Hard tissues found within Paleozoic chondrichthyan teeth (from Ginter et al., 2007).

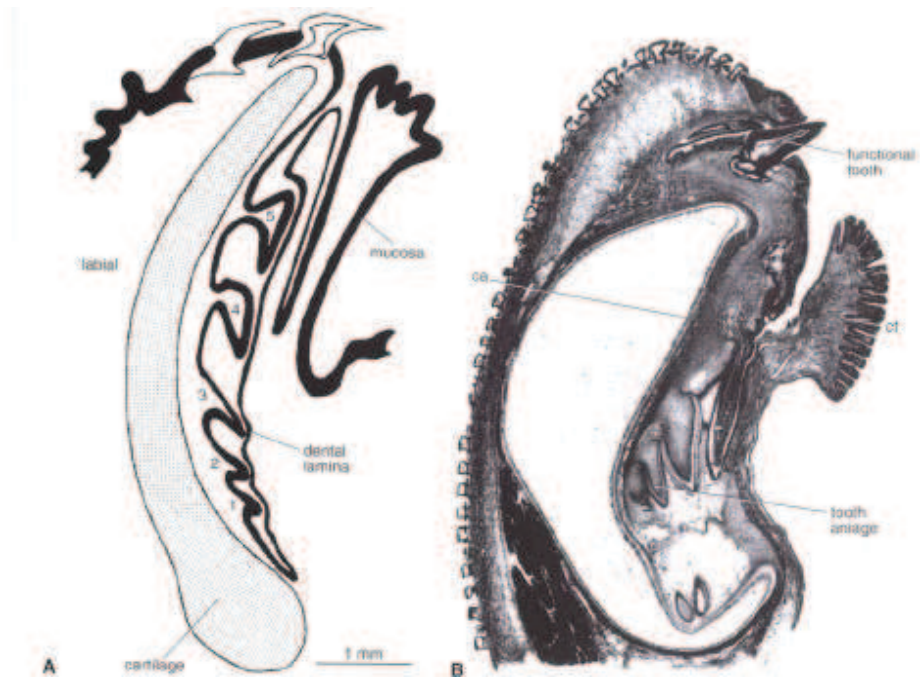


Figure 32. Chondrichthyan tooth development (from Ginter et al., 2007).

Functional teeth in chondrichthyans are backed up by rows of immature teeth forming parallel to the lingual side of the jaws. These rows of immature teeth, occupying tooth wells, and rows of functional teeth comprise the tooth battery, tooth file, or tooth family. Tooth replacement in post-Mesozoic chondrichthyans is relatively rapid. Rapidly replaced teeth show little wear. Conversely, Paleozoic chondrichthyan teeth are found often worn down, most likely from attacking prey, emptying their stomach contents from material that was hard to breakdown into usable nutrients (shells, scales, teeth, bones), or injury from one of the opposing dentitions. The overall condition of Paleozoic teeth points to slow tooth replacement of functional teeth. It has been hypothesized that the slow dentition turn-over in the Paleozoic chondrichthyans may have resulted from aspects of water chemistry, i.e., lower levels of available calcium and phosphate, needed to make teeth at a rapid pace (Zangerl, 1981; Carroll, 1988).

Dermal denticles are often preserved in the fossil record. Denticles have a thin walled cone of dentine, which is covered by a layer of enamel, with a base composed of dentine. Early chondrichthyan dermal denticles may have developed from lepidomoria, the simplest type of scales. Lepidomoria formed aggregates where individual lepidomorium fused their bases to form one continuous base, called cyclomoria (Carroll, 1988). These denticles formed on the flanks and the dorsal portions of the body. However, the dorsal denticles were complex and very durable. Their durability has led to their high preservation potential within many Late Paleozoic sedimentary units. Along the dorsal area of the body dermal denticles were added both anteriorly and posteriorly, with the posterior denticles being less specialized. Stensio (1961, 1963) and Gross (1973) have proposed that these complex denticles led to the modern placoid scales seen on



Chondrichthyes today. For a more detailed explanation for placoid scales see Carroll (1988). Denticles alone have been used for identification of genera. For example, Wells (1944) used denticles to describe a new Chondrichthyan species, *Ohiolepis* (Fig. 33) (Fig. 34) (Zangerl, 1981).

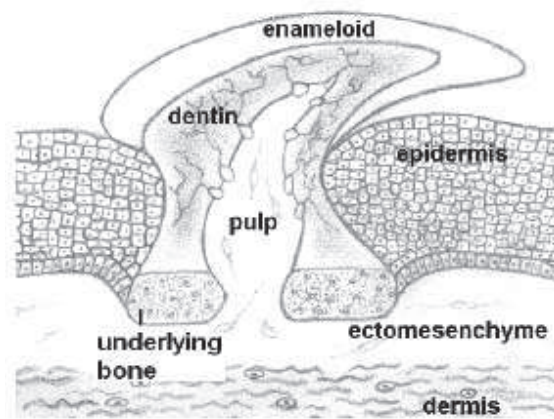


Fig. 33. Anatomy of a dermal denticle (Koussoulakou, 2009).



Figure 34. *Ohiolepis newberryi* type specimen.

Spines can also be observed in the fossil record. Spines are thought to have originated from a single enlarged dermal denticle. Spines have a structure composed of an inner layer and outer mantle. The inner layer acts as an anchor, inserted deep into the body. The outer mantle is composed of vitrodentine. The outer mantle plays a crucial role in the identification of genera. In some genera the outer mantle is composed of trabecular dentine. Trabecular dentine lacks the superficial enameloid found on denticles, thus the spine doesn't protrude the epidermis. *Cladoselache* and *Stethacanthus* both have an outer mantle composed of trabecular dentine indicating that their spines did not project out of their epidermis (Zangerl, 1981; Carroll, 1988).

The subclass Elasmobranchii (Bonaparte, 1838) differs from the subclass Holocephalia in many important anatomical characters, including the enlargement of the branchial basket in a posterior direction, wider spacing between the gill arches, and separate, lateral opening to the gill pouches, an operculum, and an axial pectoral fin which consists of both axial and radial components. Elasmobranchii also differ, most notably, in having palatoquadrates that are not fused to the neurocranium, and scapulocoracoids that are located relatively far behind the occiput (Zangerl, 1981).

Paleozoic remains of elasmobranchs are better known and better understood, than the holocephalians, yet the phylogenetic relationships of the groups within the elasmobranchs are difficult to establish because of the lack of shared-derived characters (Zangerl, 1981).

The Superfamily Protacrodontidea (Zangerl 1981) had a dermal skeleton consisting of compound scales that resemble those of acanthodians, but are much larger. The palatoquadrate is cleaver shaped. The teeth which do not form a tooth pavement are orodontid, having a main cusp flanked on either side by smaller cusps, where all cusps are heavily ridged. At the present, these elasmobranchs are placed among the Ctenacanthoid sharks, yet they lack the defining fin spines. There are also arguments to place the protocrodonts within the Order Orodontidae because of the resemblance of tooth anatomy, yet their dental crowns consist entirely of orthodentine unlike the orodontids (Fig. 35) (Zangerl, 1981; Turner, 1982; Ginter, 2001; Ginter, 2002).

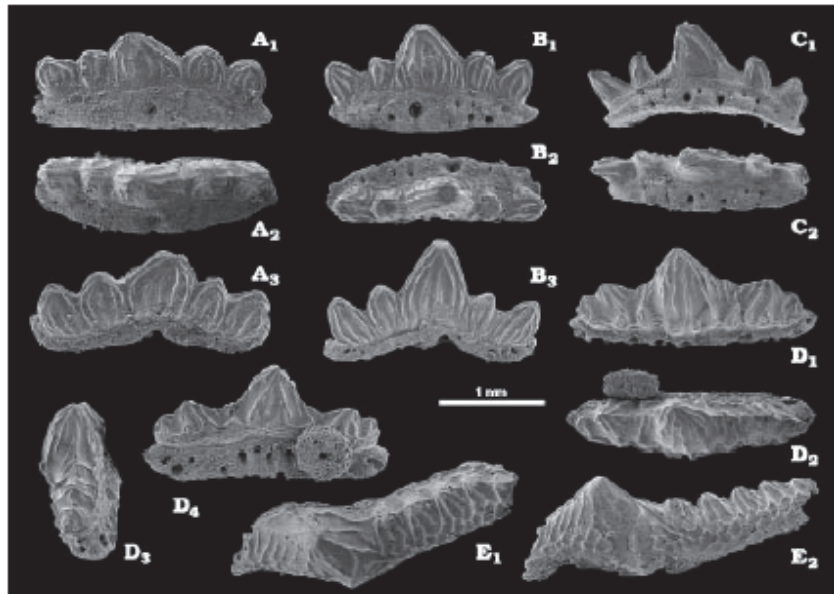


Figure 35. Examples of different *Protacrodus* sp. found in the Middle Tournaisian of Muhua, China in the Muhua Formation (from Ginter et al., 2007).

Protocrocodonts have been found in Middle to Upper Devonian rocks of Eurasia and North America, as well as the Pennsylvanian deposits of North America (Zangerl, 1981). Protocrocodont remains are typically found mainly in rocks that indicate a shallow water origin (Ginter, 2002). For example, protocrocodont remains have been found in China and Belgium, in siliciclastic-carbonate deposits which indicate a shallow water depositional environment (Lelievre and Derycke, 1998). *Protacrodus* sp. remains have also been found in the Kilbride Limestone Formation which contains abundant broken crinoid fragments indicating a moderately shallow, high energy carbonate shelf (Duncan, 2006).

Chondrichthyan teeth, denticles, and spine assemblages can be used as biofacies indicators. If more than twenty-five percent of the total ichthyoliths in a deposit belong to protocrocodonts, then the facies can be interpreted as having a shallow water origin. The tooth morphology and functional anatomy of protocrocodont dentition indicates a diet of shelled invertebrates most likely associated with carbonate shelves (Ginter, 2001).

Cladoselachians have been extensively studied due to the relatively large number of well preserved whole and partial skeletons found within concretions of the Cleveland Shale. Many of the specimens of cladoselachians that have been found belong to a single genera, *Cladoselache*, but a less common genera, *Monocladodus* Claypole 1893, has also been described (Fig. 36) (Zangerl, 1981).

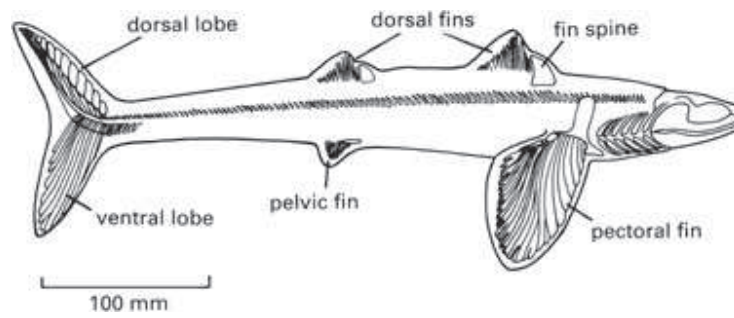


Figure 36. Cladoselachian external anatomy (Benton, 2005).



The Cladoselachidae are characterized by their fusiform body shape, blunt snouts, two dorsal fins, strongly, forked caudal fin, no anal fin, and relatively primitive paired pectoral fins. Cladoselachians are comparable to modern fast swimming pelagic sharks and bony fish with their configuration of fins and overall body shape. Multicusped denticles surround the margins of the fins and the orbits of the eyes. A relatively large otico-occipital region can be found in the neurocranium. The neurocranium houses a relatively large otico-occipital region and cleaver shaped palatoquadrates that lie behind the occipital condyles. Amphistylic jaw suspension contains cladodont style dentition; flat, semicircular bases supporting several pointed cusps, the central cusp being the largest, varying from monocuspid *Monocladodus* to polycuspid *Cladoselache* (Fig. 37) (Romer et al., 1976; Zangerl, 1981; Carroll, 1988; Maisey, 1989; Maisey, 1996; Ginter, 2001).

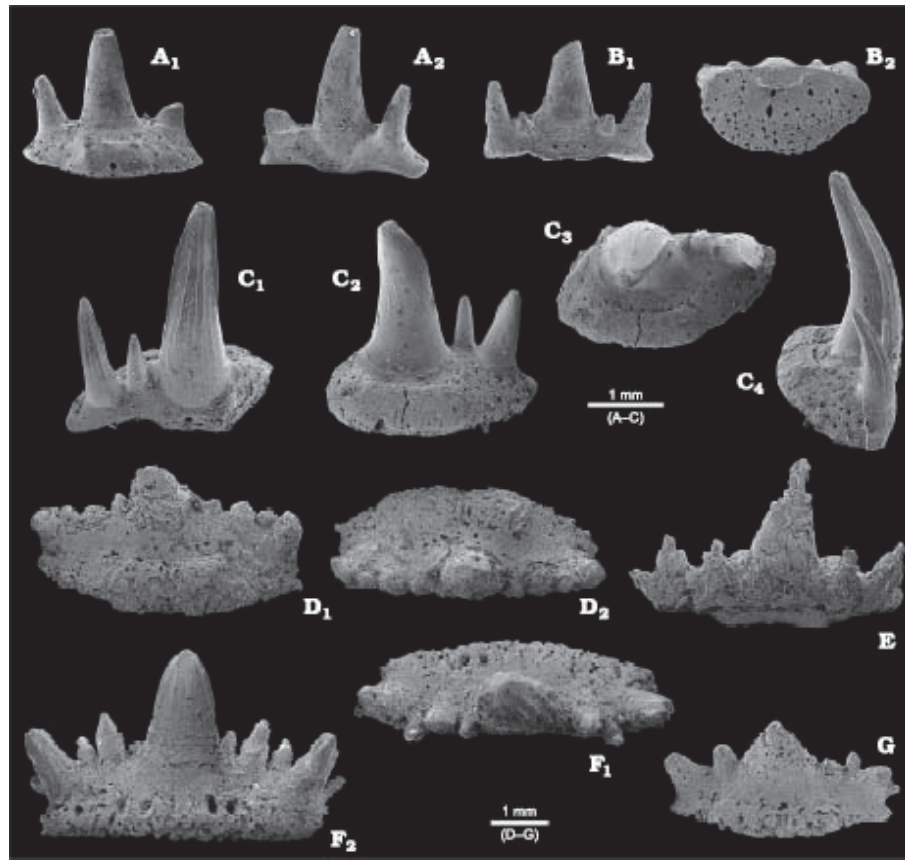


Figure 37. Different cladodont style teeth found in the Middle Tournaisian of Muhua, China in the Muhua Formation (Ginter et al., 2007).

Members of the Order Symmoriidae have a fusiform body shape, deeply forked caudal fins and a terminating mouth. Dermal denticles can be found along the lateral line, otherwise the body is naked. The symmoriids have no anal fin and have one dorsal fin located over their pelvic area. Symmoriida share many primitive characteristics with those of Cladoselachidae but differ with the nature of the fins and the absence of traditional spines, with symmoriids lacking fin spines altogether (Zangerl, 1981; Carroll, 1988; Duncan, 2006).

*Cobelodus* (Zangerl, 1973) grew to 150 to 200 centimeters in length. They had cladodont style teeth in the lower jaw only. The teeth on the palatoquadrate were long, needle-like teeth. Although there are proportional differences, the post-cranial skeleton is very similar to a *Symmorium* sp. (Zangerl, 1981; Duncan, 2006).

*Symmorium* was on average about the size of *Cobelodus* (150-200 cm in length). The teeth are of cladodont style with large bases and thinly striated cusps. A central cusp is flanked by either one, two or three pairs of lateral cusps (Zangerl, 1981; Long, 1990; Lelievre et al., 1998; Ginter, 2002).

Symmoriid skeletons are very similar to those of the stethacanthids. Stethacanthids differ by a modified spine that lacks an outer covering of orthodentine. This spine is associated with a brush-like apparatus that is covered in dermal denticles. Several functions of the brush-like complex have been proposed. These include warding off predators by flaring up the brush-like apparatus, or for mating displays (Fig. 38) (Williams, 1979; Zangerl, 1981).

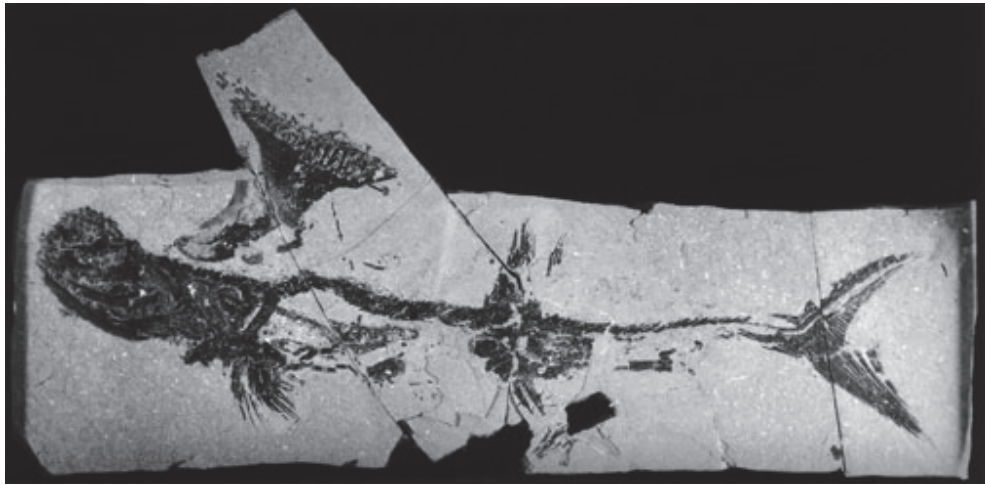


Figure 38. Fossil specimen showing the unique brush-like apparatus from the Mid-Carboniferous of Bearsden, Glasgow, Scotland (Benton, 2005).

Teeth of *Stethacanthus* are similar to *Symmorium*, with the exception that *Stethacanthus* teeth are usually larger. Most of the body features observed in *Stethacanthus* are identical to the body features observed in *Symmorium*, including scapulocoracoid and the vertebral column along the trunk region. Due to the close similarities between these two genera it has been thought that *Symmorium* is the female form of *Stethacanthus*. Female forms of *Stethacanthus* sp. have not been observed, meaning all skeletons, where identifiable, have been observed with claspers. Male forms of *Symmorium* sp. have not been observed, meaning all skeletal remains, where identifiable, had no clasper organs (Zangerl, 1981; Lelievre et al., 1998; Ginter, 2002).

Family Phoeodontidae (Williams 1979) includes only one member, the genus, *Phoeodus*. *Phoeodus* remains include partial skeletons and teeth. The teeth are of cladodont style. The central cusp is no longer than the lateral cusps. The lateral cusps are tilted away from the central cusp at angles of thirty and forty-five degrees (Zangerl, 1981). The teeth of *Phoeodus* were designed to function for grasping prey. *Phoeodus* most likely preyed on small fish and unarmed cephalopods (Ginter, 2001). *Phoeodus* is a spiny elasmobranch, with cleaver shaped palatoquadrates. The pectoral fins are dibasal or tribasal. The first fin spine is larger than the second. The skin is covered in dermal denticles. *Phoeodus* teeth have been found in strata from the Middle Devonian through the Upper Carboniferous (Zangerl, 1981; Turner, 1982; Ginter, 1990; Long, 1990; Lelievre et al., 1998; Ginter, 2001; Ginter, 2002).

Phoeodontiids mostly occupied open, moderately shallow to moderately deep, well oxygenated waters (Ginter, 2002). Ginter has proposed using chondrichthyan ichthyolith biofacies to determine depositional environments. If twenty-five percent of the

taxa are remains of *Phoebodus* and *Thrinacrodus*, then the depositional setting can be interpreted as moderately deep shelves (Ginter, 2001), thus meaning *Phoebodus* lived in moderately deep waters.